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**THE ECOLOGICAL IMPACT OF RECREATION
IN BRITISH TEMPERATE WOODLANDS**

by

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A thesis submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy

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Environmental Sciences and Education Research Unit, Institute of Education

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Any maps, pages, tables, figures graphs, or photographs, missing from this digital copy, have been excluded at the request of the university.

For my parents

*'They shut the road through the woods
Seventy years ago.
Weather and rain have undone it again,
And now you would never know
There was once a path through the woods
Before they planted the trees,
It is underneath the coppice and the heath,
And the thin anemones.
Only the keeper sees
That, where the ring-dove broods,
And the badger rolls at ease,
There was once a road through the woods'.*

*from The Way Through The Woods,
Rudyard Kipling*



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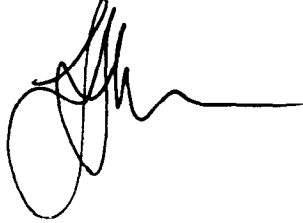
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Declaration

I declare that the work presented in this thesis has not been submitted for a degree at any other University. An informal article based on the general conclusions of Chapter 3 was published in the spring 1997 edition of *Tree News*.

I declare that I am the sole author of this thesis.

A handwritten signature in black ink, consisting of a large, stylized 'O' followed by a series of loops and a long horizontal stroke extending to the right.

Summary

In recent decades, the ecological impact of recreation in woodlands and forests has been a subject of considerable world-wide interest. However, there are few studies examining the effects of recreation on woodland vegetation, soils and fauna in Britain.

This thesis identifies recreational trampling as a major contributor in facilitating ecological change in urban fringe semi-natural ancient temperate woodlands of Warwickshire, England. Relationships with trampling intensity are generally curvilinear, suggesting that the rates of damage are most rapid at initial stages of trampling. Biotic communities are shaped so that their structure and diversity is related to the type, intensity and frequency of impact.

The impact of trampling on vegetation is the most precise indicator of recreational use. Multi-variate analyses indicates that trampling is the primary organisational gradient operating on ground vegetation, with trail centres dominated by secondary plant associations at equilibrium with the trampling pressure. Trail margins are dominated by vegetation that is tolerant of low levels of trampling *and* high rates of competition.

Experimental trampling experiments show that the ecological carrying capacity of woodlands for recreation are lower than previously thought; from below 150 people per year in *Rubus fruticosus* agg. and *Pteridium aquilinum* dominated stands to below 75 people per year in coniferous stands with *Hyacinthoides non-scripta* ground flora.

The ability of vegetation to tolerate trampling is related to plant anatomy, morphological adaptations, plant strategies, growth rate, position of the perennating bud, environmental conditions such as canopy density and is more a function of the ability to recover from trampling rather than to resist. By virtue of their delicate morphology, stands dominated by shade tolerant species are the most vulnerable to trampling.

Increases in soil compaction and decreases in pore space and oxygen content are recognised as important in shaping woodland vegetation and fauna, and the reduction in soil inhabiting invertebrate and micro-organism populations have consequences for woodland processes. A bioindicator index to assess soil damage is provided using Acari body length.

Models summarising the ecological changes associated with trampling and the ecological carrying capacity of woodlands are provided, along with a woodland management checklist and an index of vulnerability for resource managers to assess the potential of woodland stands to withstand recreational use.

Chapter 1

INTRODUCTION

1.1 Recreational use of Britain's woodlands

Temperate deciduous woodland is the natural climatic-climax vegetation of Britain, covering just 4 % of the land area (Green 1992). Many of these woodlands are small fragments located on the urban fringe, yet offer unparalleled scope and opportunities for the multi-purpose activities of recreation and forestry practices to occur together. Recreation creates as many problems for wildlife habitats as intensive farming or forestry (Tait *et al.* 1988), so the conservation goals of many important woodland sites are compromised by anthropogenic disturbances. Furthermore, most forms of recreational activity are incompatible with priorities for wildlife (Speight 1973), and over use and lack of management will eventually lead to the degradation of species rich areas of high prior conservation value (Goldsmith 1983a, Liddle 1975a). Recreational use has been identified as a major contributor in facilitating ecological change in woodlands (Cole 1993, Taylor *et al.* 1993), with vegetation and soils particularly susceptible ecosystem components (Anderson & Radford 1992, Cole 1985, Kellomaki & Saastamowen 1975).

1.2 The concepts of recreation and formal and informal recreational use

Britain's woodlands and forests are a highly valued free recreational resource, and provide benefits for people's physical and mental well-being. The most common forms of recreational use are simple and pursued close to the home often as a part of daily life. The 'recreational use' of woodlands in the context of this study is defined as - 'a use for leisure purposes in any kind of formal or informal activity from which people feel they derive mental and / or physical satisfaction'.

The attraction of woodlands to the public is by virtue of their aesthetic quality, wildlife diversity, age structure, type and size of the trees and presence of features such as open glades and rides. Accordingly, the principal woodland resources of open glades, footpaths, tracks and rides are commonly used for informal recreational activities such as hiking, picnicking, dog walking, children playing, horse riding, jogging, mountain biking and wildlife watching. Woodlands are also the preferred

location for formal organised events such as orienteering, paintball wargames, guided walks, conservation work parties and school visits. Formal recreational activities generally occur less frequently than informal activities, but use tends to be more intensive. Urban fringe woodlands are also used for anti-social and occasionally illegal activities such as vandalism, the abuse of drugs and alcohol, rubbish tipping, homes for vagrants and motorbike scrambling.

1.3 Current recreational demand

The demand for recreation in the woodlands and forests of the British Isles is set to increase (Anderson & Radford 1992), with Britain's woods and forests receiving a staggering 346 million visitor days in 1996 (Anderson 1997). There is added pressure on urban fringe woods from the largely urban based population, although increases in leisure time and private vehicle ownership over the last three decades have contributed to a general increase in recreational usage of the British countryside. By calling for '*greater freedom for people to explore our open countryside*', the ramifications of the recent Labour Party manifesto (1997) on future demand must also be recognised. At current levels of demand, the considerable pressure of recreation and access threatens the ecological integrity of woodland ecosystems.

1.4 The ecological impact of trampling on woodlands

The causal agents of trampling originate from the passage of feet from people or other large mammals, and is linked with three main impacts:

- the deterioration of ground vegetation
- changes to soil conditions
- the disturbance of animals

By far the most common recreational impact is trampling derived from people walking. Liddle (1984) identified three key stages in the trampling process as *alpha* (the initial sight of a plant by the trampler with a choice to prefer or avoid vegetation,

and thus create new paths), *beta* (actual physical contact and subsequent amounts of damage) and *gamma* stages (recovery of ecosystem). During the *beta* stage, there are six subdivisions of gait, including shearing, crushing, toe and heel gouging, grinding and ripping actions (Holmes & Dobson 1976). Each of these actions applies different vertical and dynamic forces to the ground. The use of animals or vehicles for transport generally increases pressures by 5 to 10 times in comparison with those exerted by walkers (Liddle 1997). The impact of trampling from a single or a combination of these factors inflicts physical damage to woodland biota and soils.

Some of the most visually evident impacts attributed to trampling act upon vegetation, where damage eliminates sensitive plant species and causes reductions in vegetation cover, height, biomass and growth rate, species number, species diversity and root systems (Bates 1935, Cole 1988, Cole & Bayfield 1993, Liddle 1973, 1975a, 1975b, Liddle & Thyer 1986, Makhdoum & Khorasani 1988). Plant cover loss is generally the most obvious change, and tends to decrease in worn areas where only resistant species can survive (Liddle 1975b). Species tolerant of moderate levels of trampling can colonise certain areas, but tend to survive in transition between heavy trampling stress and being out-competed by taller vegetation on path margins (Liddle 1975b). In association with changes to vascular plants, fungi (*Dokukina*⁷ 1992, Westhoff 1966⁷) and lichens (Bayfield 1971b, Bayfield *et al.* 1981, Willard & Marr 1970, 1971) are particularly vulnerable to trampling.

Heavily trampled tracks and paths also provide visual evidence of trampling, where accelerated soil erosion rates result in widespread footpath deterioration (Bayfield 1979^a, Burden & Randerson 1972, Chappell *et al.* 1971, Speight 1973). Trampling inflicts changes to the physical properties of soils by increasing levels of compaction, bulk density, run-off and the exposure of mineral soil (Bright 1986, Cole 1987, 1988, Dale & Weaver 1978⁴, Dunn 1984, Kuss & Hall 1991), and decreasing pore space, infiltration rates and aeration properties (Aspinall & Pye 1987, Burden & Randerson 1972, Makhdoum & Khorasani 1988).

Finally, the impacts on fauna are less subjectively obvious, but trampling induces direct mortality and indirect changes to habitats where fauna live and breed, e.g.: birds (e.g.: Van Der Zande^{et al.} 1984), invertebrates (e.g.: Bayfield 1979b) and micro-organisms (e.g.: Duggeli 1937). Specific recreational activities also induce direct changes to populations of larger animals, for instance by shooting, hunting and fishing.

The introduction attempts to review current working knowledge of the ecological impacts of recreational trampling on woodland biota and soils, and acts as a basis for the synthesis of aims and objectives that are set out in section 1.5.

1.4.1 *The effects of trampling on woodland vegetation*

1.4.1.1 *Woodland ground flora*

~~Most~~ ^A authors are in universal agreement that forest and woodland ground flora is particularly vulnerable to trampling (Kellomaki 1973, Kellomaki & Saastamowen 1975, Rogova 1976). World-wide studies conclude that the sensitivity of woodland vegetation to trampling is directly related to species morphology, anatomy, phenology and physiology, and environmental factors such as climate, canopy cover, slope, soil type and moisture status (e.g.: Kuss 1986, Liddle 1975b, Speight 1973).

Woodland vegetation responds poorly to trampling because species growing in moist or wet habitats are more sensitive to recreational impacts than those growing in drier habitats (Emanuelsson 1983, Kellomaki & Saastamowen 1975, Kuss 1986, Leney 1974). Indeed, woodland species adapted to the conditions of environmental stress imparted by impoverished light regimes are extremely susceptible to physical damage from trampling (Anderson & Radford 1992, Chadee 1988, Cole 1979, 1985, 1987, 1993, 1995b, Marion & Merriam 1985, Schreiner & Moorhead^b 1979). Their poor response is strongly related to vulnerable morphology (Cole 1979, Kuss 1986).

The relationships between trampling intensity and vegetation response (most notably cover and biomass) have been shown to be curvi-linear for most woodland vascular

plants (Cole 1985, 1987, 1988, 1995a, Dale & Weaver 1974, Frissell & Duncan 1965, Kellomaki 1973, Kellomaki & Saastamowen 1975, Wagar 1964), and linear for mosses (Cole 1985). Highly curvi-linear relationships are prevalent in vegetation types that are particularly susceptible to trampling, whilst relationships for more resistant vegetation types are linear (Cole 1995a). Deterioration is greatest at the lowest level of trampling (Bell & Bliss 1973, Cole 1995a, LaPage 1967), so that ^{in curvilinear} ~~relationships~~ further successive increases in trampling intensity have a progressively lower impact on the rate of cover loss (Cole 1985).

1.4.1.2 *Trees*

There is limited evidence to suggest that mature tree health problems are associated with damage from trampling, but tree species growing adjacent to trail systems may suffer from damage to exposed roots. For example, LaPage (1962) found a decrease in tree trunk diameter for species located on recreation sites, and Wisdom (1988) found some localised damage around tree bases associated with combat games in woodlands. Damage to tree roots occurs because dead roots are visible in areas of excessive compaction (Bryan 1977, Burger 1932), although they are generally scarce in the upper 15 cm of compacted soils (Settergren & Cole 1970). However, even though highly compacted soil restricts roots to cracks and inhibits root elongation, it is possible that very low levels of trampling can enhance root firmness and even increase plant growth rates (Dunn 1984).

1.4.1.3 *Factors that control vegetation vulnerability to trampling*

1.4.1.3.1 *Vegetation characteristics*

The variation in the ability of species to tolerate trampling conditions has long been recognised. The two main causal factors related to woodland plant tolerance of trampling are:

- initial destruction of biomass

- subsequent regeneration of biomass

Relationships are dynamic and are affected by the intensity, frequency and timing of trampling (Kellomaki & Saastamowen 1975).

The strategies employed by species that are advantageous in resisting physical damage caused by trampling are listed in Table 1.1, along with features that make other species intolerant.

1.4.1.3.2 The concept of plant strategies

The vulnerability of vegetation to trampling can be quantified by using the properties of plant strategies because they can be directly applied to different phases of human / plants interactions (Liddle 1997). Plant strategies are defined by Grime (1979) as *'groupings of similar or analogous genetic characteristics which recur widely amongst species or populations and cause them to exhibit similarities in ecology'*. Plant strategies influence the resistance, survival, recovery and overall tolerance of vegetation.

Sun & Liddle (1993c) defined 'resistance' as *'the ability of a species to maintain its physical structure when subjected to trampling'*. Plant strategies which increase resistance to trampling include creeping, low growing, rosette, tussock and bunched growth forms, small size, high leaf strength, flexibility of vegetative parts and phenotypic plasticity (Bates 1935, Cole 1979, Goryshina 1983, Grabherr 1983, Holmes & Dobson 1976, Kuss 1986, Liddle 1975a, 1991, Naito 1969, Pryor 1983, Speight 1973, Sun & Liddle 1991, 1993a, 1993b, 1993c, Willard & Marr 1970).

'Survival' is the probability of survival after a given amount of time (Sun & Liddle 1991). Bayfield (1979a) defined three categories of survival strategists;

- the most susceptible (high amounts of damage and poor recovery)
- moderately susceptible (moderate to high initial damage, fairly good recovery)
- low susceptibility (low to moderate damage and an increase in cover).

'Recovery' is defined by Liddle & Kay (1984) as *'the growth rate of an organism after a given amount of damage expressed as a proportion of the growth rate of the*

Table 1.1 - Features that contribute to vegetation tolerance or intolerance of recreational trampling.

	Trampling tolerant	Trampling intolerant
Growth rate	rapid	variable
Class	mainly monocots	mainly dicots
Stem architecture	short, trailing procumbent, flexible, tufted, bunched, thorns, prickles	tall, succulent, erect, brittle, woody branches
Leaf architecture	flat, basal, tough, pliable, whorled, rosette, folded, narrow, wiry, tufted	thin, broad, long petiole, delicate, caulescent shoots
Growth-form	low growing, matted, tufted, small stature, growth from intercalary as well as apical meristems, underground perennating organ, regenerate by layering, large root mass, ability to reproduce vegetatively	erect, tall stature, shallow roots, single exposed perennating organ, adapted to severe competition in moist conditions
Life-form ^a	cryptophytes, hemicryptophytes	phanerophytes, chamaephytes
Examples	mosses, graminoids (grasses, rushes, sedges)	woody shrubs, forbs, ferns, herbaceous species, lichens, tree seedlings, climbers, succulents, bog moss

^a - based on life-form classes recognised by Raunkiaer (1934)

(Compiled from: Bates 1935, Cole 1982,1983,1985,1987,1993,1995b, Cole & Trull 1992, Dale & Weaver 1974, Del Moral 1979, Hall & Kuss 1989, Holmes & Dobson 1976, Kellomaki & Saastamowen 1975, Kuss 1986, Liddle & Grieg-Smith 1975b, Liddle & Thyer 1986, Naito 1969, Price 1983, Rogova 1976, Schreiner 1974, Singer 1971, Slatter 1978, Speight 1973, Studlar 1980, Wagar 1964, Weaver & Dale 1978, Yorks *et al.* 1997).

control'. Characteristics of recovery strategists include a densely branched or tussock growth form, rapid growth and recovery rates, efficient regenerative properties and the ability to tolerate enhanced competition (Grime 1979, Sun 1992).

However, the overall ability of a plant sub-community to tolerate trampling is related to resistance, survival *and* recovery. Such a measure is defined as 'tolerance', which is affected by degree of woodiness, flexibility, erectness, height and density, location, size and strength of stems and leaves (Cole 1987).

Morphology and phenology also provide clues to species response, with growth rates, environmental factors, reproductive capacity and the position of the perennating bud all critical (Cole 1987). Other factors include the length of growing season, associated vegetation, vegetation layering, graminoid component, natural senescence, high seed years, plant turgor, delayed damage, reproduction by suckers, stolons, corms, tubers, rhizomes and bulbs and the extent of the root system (Anderson & Radford 1992, Cole 1987, Holmes & Dobson 1976, Leonard *et al.* 1985, Liddle 1975b, Speight 1973).

1.4.1.3.3 Environmental characteristics

Soil type, soil moisture status and absorptive capacity, nutrient availability, microtopography, aspect, elevation, slope and habitat preferences all affect the ability of vegetation to tolerate trampling (Cole 1988, Kellomaki & Saastamowen 1975, Kuss 1986). The presence of a canopy overstorey retains moisture, produces cooler temperatures, higher humidities and reduces the quantity of photosynthetically active radiation reaching the forest floor (Kuss 1986). Heavily shaded conditions are a major limiting factor for plants of the shrub, herb and bryophyte layers (Grabham & Packham 1983), and ^{may} produce a woodland floor devoid of vegetation with a high proportion of bare ground (Schreiner & Moorhead 1979^b, Ripley 1962). The net result of conditions of high environmental stress mean that vegetation in densely forested sites is more fragile than in open sites (see section 1.4.1.1).

Increasing levels of soil compaction provide an environment that is competitively advantageous to the seedling establishment and tillering capacity of some plant species, and can virtually eliminate competition from others (Kuss & Hall 1991, Liddle 1973, 1975b). Light levels of trampling may also scarify the soil surface, and

create a more favourable seedbed (Leonard *et al.* 1984³). Generally however, trampling induces seedling mortality in most plants. For example, the seedling density of *Pinus edulis* was found to be reduced by 73 % in heavily trampled areas compared to lightly trampled areas (Tonnerson & Ebersole 1997).

1.4.2 *The consequences of recreational trampling on woodland fauna*

1.4.2.1 *Woodland birds and mammals*

The potentially disturbing impacts of recreation on woodland birds is recognised by Hearn (1981), who described them as one of the most vulnerable features of oak woodlands. Disturbance negatively affects fecundity and densities of the more common bird species in urban woodlands, and is related to the incidence and nature of the impact with respect to the breeding season (Sidaway 1990, Verstrael in Ferris-Kaan 1991). However, the affects of recreational disturbance on the breeding success of overwintering, ground nesting birds, concepts of territoriality and the impacts of specific recreational activities are not widely documented.

Small mammals are also sensitive to disturbance where trampling pressure has destroyed overlying vegetation cover and diminished the availability of suitable invertebrate prey items. Indeed, Wisdom (1988) showed that *Sorex araneus* (common shrew) is less prolific in woodland plots prone to damage from paintball games compared to undisturbed areas. However, Foin *et al.* (1977) reasoned that large populations of small mammals should be relatively insensitive to adverse environmental conditions such as trail use. The response of other mammals are less well documented, but *Meles meles* (badger) is susceptible to disturbance, with delayed emergence and sett abandonment (Neal 1977).

1.4.2.2 *Invertebrates*

Trampling causes a decline in invertebrate species diversity, promotes an influx of scavenging species and increases the proportion of organisms normally associated

with bare ground at the expense of those associated with habitats of higher stability (Speight 1973). Impacts of recreational trampling on soil inhabiting fauna are both direct, from the physical forces of treading, and indirect, by changes to micro-habitat and edaphic conditions. Speight (1973) deduced that the impact of trampling is more severe on invertebrate species associated with woodland ground flora compared to woodland vertebrates. A preliminary investigation of the effects of recreation on woodland invertebrates is hampered by rather poor documentation in Britain, and there appears to be only one relevant study (see Wisdom 1988).

Hunting, fishing, shooting, active habitat management procedures and specimen collecting (especially bird eggs and Lepidoptera) are other notable problems associated with recreation in woodland. The removal of dead wood for construction of camps, dens, brash and firewood also has consequences for certain invertebrate groups (Webster & Adams 1989).

1.4.2.3 *Micro-organisms*

Soil micro-organisms help to regulate decomposition and nutrient cycling processes in woodland habitats, and so impacts associated with recreation that change the structure and diversity of communities can adversely affect soil fertility and thus woodland productivity (Bengtsson *et al.* 1997, Madden & Fox 1997). Micro-organism populations and soil pore size, water content, aeration properties, temperature, nutrient availability all appear to be inter-related and are negatively impacted upon by compaction from recreation (De Gouvenain 1996).

Duggeli's (1937) pioneering study in Zurich indicated that soil bacteria are generally twice as abundant in undisturbed woodland soils compared with trampled soils. There is a change in community composition, with the eradication of nitrifying bacteria and an increase in denitrifying forms (Duggeli 1937, Speight 1973). Dunn (1984) considers indirect changes such as microclimatic variation caused by trampling to be of greater influence on micro-organisms than direct physical damage from treading.

1.4.3 Effects of trampling on woodland soils

Throughout recorded history, the impact on soil by people has always been a detrimental one (Hodges & Arden-Clarke 1986). This dates from as far back as three million years ago, when the Olduvai cave dwellers used a home centre reference system to retrace familiar routes, inadvertently creating the very first paths (Gatty 1958 in Liddle 1973). Indeed, ever since the first extensive evidence of pathways made approximately 5000 years before present (Coles & Hibbert 1968 in Liddle 1973), the use of established trail networks has led to profound changes in soil properties. The response of the physical environment to these changes is dependent upon soil type, slope, aspect, species composition, weather conditions, seasonality, geology and the past management regime (Burden & Randerson 1972).

Table 1.2 summarises the general response of woodland soil properties to trampling pooled from available literature, and the reviews by Anderson & Radford (1992) and Dunn (1984) highlight the general impact of recreational trampling on woodland soils.

1.5 Aims and objectives

The purpose of this thesis is to quantify the ecological impact of recreational trampling on biota and soils in lowland, temperate semi-natural ancient deciduous woodlands. Emphasis is placed on addressing Liddle's (1997) recent call for:

- an extension to our basic knowledge of the effects of recreation impacts
- a greater amount of research tackling management problems
- the communication of these results in a form that can be immediately digested by land managers

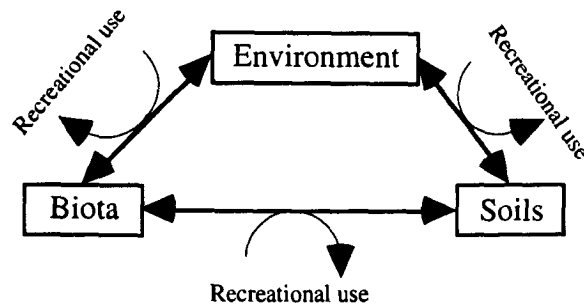
There are three main research objectives:

- i). To examine the influence of recreational use on the nature of the inter-relationships between the ecosystem components identified in Fig. 1.1. As there are relatively few studies examining the effects of recreation on British

Table 1.2 - Summary of the effects of recreational use on woodland soils (properties in **bold** increase with trampling, and those in *italics* decrease with trampling).

Soil property	Authors
• compaction	(Adkinson & Jackson 1996, Cole 1985, 1987, 1988, Dunn 1984, Kuss & Hall 1991, Kuss 1986, LaPage 1962, Leonard <i>et al.</i> 1985, Magill & Nord 1963, Rogova 1976, Young & Gilmore 1976)
• bulk density	(Cole 1982, Dotzenko <i>et al.</i> 1967, Ingellog <i>et al.</i> 1977, Legg & Schneider 1977, Parikesit <i>et al.</i> 1995, Settergren & Cole 1970, Thorud & Frissell 1976)
• bare ground and soil exposure	(Burden 1970, Cole 1985, 1988, 1993, Cole & Marion 1985, Weaver & Dale 1978)
• trail width	(Bright 1986, Dale & Weaver 1974, Leonard <i>et al.</i> 1985, Weaver & Dale 1978)
• root exposure	(Burden 1970, Cole 1982, Settergren & Cole 1970)
• extent of erosion	(Barker 1967, Burden 1970, Settergren & Cole 1970, Speight 1973)
• drainage impedance	(Cole 1982, Ferrero 1991, Kuss 1986, Lutz 1945, Webster & Adams 1989)
• water content (in dry conditions)	(Burden 1970, De Gouvenain 1996, Dunn 1984, Lutz 1945, Wisdom 1988)
• soil nitrogen	(Dunn 1984, Parikesit <i>et al.</i> 1995, Young & Gilmore 1976)
• soil pH	(Dunn 1984, Ingellog <i>et al.</i> 1977, Parikesit <i>et al.</i> 1995, Young & Gilmore 1976)
• <i>pore space and macro-porosity</i>	(Burden 1970, Ingellog <i>et al.</i> 1977, Legg & Schneider 1977, Lutz 1945)
• <i>aeration and oxygen content</i>	(Burden 1970, Duggeli 1937, Lutz 1945, Meinecke 1929)
• <i>horizon depth</i>	(Dunn 1984, Ingellog <i>et al.</i> 1977, Legg & Schneider 1977, Weaver & Dale 1978)
• <i>litter cover and organic matter content</i>	(Adkinson & Jackson 1996, Bright 1986, Cole 1982, 1987, Dotzenko <i>et al.</i> 1967, Legg & Schneider 1977, Liddle & Thyer 1986, Parikesit <i>et al.</i> 1995, Young & Gilmore 1976)
• <i>water content (in wet conditions)</i>	(Dunn 1984, Settergren & Cole 1970, Wisdom 1988)

Fig. 1.1 - Interactions between ecosystem components and recreational use



woodland soils, vegetation and fauna (Anderson & Radford 1992), dynamic ecological relationships are only partially understood.

- ii). To estimate the carrying capacity of woodlands for recreation. The ecological response of woodland ecosystems to recreational use suggest that studies of recreation ecology can provide quantitative estimates of woodland ecological carrying capacity. In the context of recreational access, the definition of carrying capacity is modified from Speight's (1973) as - *'The maximum intensity of use by specified forms of recreational activity, measured in terms of numbers of people per year a given area will support without undergoing an unacceptable degree of ecological change away from the ecosystem condition considered desirable'*. By determining the site carrying capacity, the protection of sensitive sites can be assured by identifying the most resistant features of a woodland, and then manipulating visitor use patterns below the maximum level required before permanent damage takes place (Cole 1987, Rogova 1976).
- iii). To use the applied ecological investigations as a basis for the development of management strategies that minimise the conflicts between conservation and recreational use.

This thesis consists of five separate investigations, a general discussion and a final section relating the ecological conclusions to the management of woodlands for recreation. The first chapter surveys vegetation and soils of trails (footpaths, tracks

and rides) using a variety of fieldwork methods. Similar quantitative studies of the impact of trampling on woodlands have been made by Adkinson & Jackson (1996) and Parikesit *et al.* (1995). The second chapter attempts to quantify the carrying capacity of ~~specific ground flora sub-communities~~ and soils using an adaptation of the experimental trampling trials by Cole & Bayfield (1993). Paralleling research in United States forests by Cole (1985, 1988, 1993), the effects of wear and the rate of recovery of biota are measured in previously undisturbed areas. A third chapter examines the impact of simulated trampling carried out in a series of glasshouse based experiments on typical footpath and woodland plant species. This work attempts to further the understanding of plant strategies that convey tolerance to trampling, and complements work on tropical and sub-tropical grassland species by Sun & Liddle (1991) and Sun (1992). The fourth chapter examines the impact of trampling on the chemical and physical properties of woodland soils, and the fifth chapter investigates impacts on soil and litter dwelling invertebrates and micro-organisms. In the final chapter, the applied ecological research examined in the previous investigations is used to synthesise practical management criteria that are made with reference to amenity, recreation and conservation objectives.

By analysing the impacts of recreationists on sites, the findings of this thesis have importance when actively managing recreation areas. Final conclusions have significance at local and national levels in political and planning contexts, especially with regard to sanctioning recreational access.

Chapter 2

**LONG-TERM MONITORING OF GROUND FLORA VEGETATION
AND SOILS ALONG TRAMPLED TRAILS IN SEMI-NATURAL
ANCIENT DECIDUOUS WOODLAND**

2.1 Introduction

This chapter aims to provide a measure of the overall susceptibility of woodland ecosystems to recreational trampling because research examining changes to vegetation, soils and animals caused by trampling is extremely poorly documented (Liddle 1997). This work addresses the shortfall by monitoring changes in vegetation and soil parameters along existing woodland trails, assuming that deterioration of ground vegetation is the most visually evident impact induced by the recreational use of ecosystems (Frissell & Duncan 1965, Kellomaki & Saastamowen 1975, LaPage 1967).

2.1.1 Research objectives

- To monitor the long-term seasonal response of in-situ ground vegetation and soils of three urban fringe deciduous woodland communities to trampling along established trails (minor and major footpaths, bridleways, tracks and rides).
- To define the primary factors that account for vegetation differentiation in sampled areas by quantifying the nature of the inter-relationships between vegetation, soil and environmental characteristics.
- To investigate and account for similarities and differences in sub-community species composition, diversity and number between trail centres, trail margins and undisturbed shaded vegetation located off-trail.
- To define characteristics which convey plant tolerance or susceptibility to trampling, and to classify commonly encountered species accordingly.
- To consider plant species in terms of life-form (Raunkiaer 1934), growth form and ecological strategy (Grime 1979). These classification systems provide useful bioindicator information, as the attributes of morphology, life-history and physiology of species can be used as a tool to predict the vulnerability of vegetation and the capacity to tolerate disturbance.

- To construct logical models which relate ecosystem components with the ecological changes associated with recreational trampling, and to identify causal pathways.
- To formulate guidelines to aid the management of lowland deciduous woodlands for recreation in the British Isles.

2.2 Materials and Methods

2.2.1 Field sites

Tocil Wood, Crackley Wood and Tilehill Wood are located on the urban fringe of the City of Coventry (Plate 2.1), and are assumed to lie in the large vice-county of Warwickshire. In Warwickshire, ^{Semi-natural} woodland is the most abundant habitat, but still only covers 3 % by area (Wyatt 1993).

Crackley Wood is situated amidst agricultural land to the north of the town of Kenilworth, and its open access means that the reserve is extremely popular for local amenity use (Warwickshire District Council 1992). It is much used for dog walking, picnicking in the large woodland glades, mountain biking, fruit and nut gathering, observing wildlife and even for more sinister, anti-social activities (Thompson pers. commn. 1996). As a consequence, the wood suffers from a proliferation of heavily waterlogged and badly eroded footpaths.

Tilehill Wood is one of the largest tracts of semi-natural woodland left remaining in the West Midlands. It is situated near Tilehill in Coventry, and is surrounded on all four sides by a housing estate, factory and two schools. The woodland is open to damage from off-road vehicles, horse riding and mountain bikes. Clay soils and a high water table promote poorly drained, waterlogged paths. Fly-tipping, the creation of new, unwanted paths and fire-lighting are further problems (Clark pers. commn. 1994).

Tocil Wood is located on the University of Warwick campus near Coventry and is bisected by a cycle track and paved footpath running from east to west. This small woodland is used extensively for dog walking, cycling and jogging by students and local residents (Ware pers. commn 1997).

All three woodlands were classified according to National Vegetation Classification criteria as W10 *Quercus robur* - *Pteridium aquilinum* - *Rubus fruticosus* communities, the dominant woodland type in lowland England (Rodwell 1991) (Table 2.1).

Plate 2.1 - Location of study sites in the Coventry area of Warwickshire and the West Midlands.



Table 2.1 - Site characteristics of Tocil Wood, Crackley Wood and Tilehill Wood.

Site	Tocil Wood	Crackley Wood	Tilehill Wood
Grid reference	SP 303 764	SP 290 742	SP 280 742
Size (ha)	4.5	25	29.4
Status	Local Nature Reserve	Local Nature Reserve	S.S.S.I
Ownership	Coventry City Council	Warwick District Council / Private	Coventry City Council
Management	Warwickshire Wildlife Trust	Warwickshire Wildlife Trust	Coventry City Council Leisure Services & English Nature
Geology	Upper coal measures marl	Permian or Upper Carboniferous Kenilworth Sandstone	Red Keuper and Upper Carboniferous marl
Soil series ^a / types	Shifnall (typical brown-earths); Compton (pelo-alluvial gleys)	Shifnall (typical brown-earths); Dodmoor (stagnogleyic brown-earths)	Salop and Rufford (typical stagnogleyic brown-earths)
Canopy and shrub layer	<i>Quercus robur</i> , <i>Acer pseudoplatanus</i> , <i>Fraxinus excelsior</i> , <i>Corylus avellana</i> , <i>Ilex aquifolium</i>	<i>Quercus robur</i> , <i>Betula pendula</i> , <i>Castanea sativa</i> , <i>Sorbus aucuparia</i> , <i>Corylus avellana</i> , <i>Ilex aquifolium</i>	<i>Quercus robur</i> , <i>Betula pendula</i> , <i>Castanea sativa</i> , <i>Pinus sylvestris</i> , <i>Corylus avellana</i>
Ground flora	<i>Rubus fruticosus</i> agg., <i>Pteridium aquilinum</i> , <i>Hyacinthoides non-scripta</i>	<i>Rubus fruticosus</i> agg., <i>Pteridium aquilinum</i>	<i>Rubus fruticosus</i> agg., <i>Pteridium aquilinum</i>

^a - classified by Beard (1984)

2.2.2 Sampling method

The response of ground vegetation and soils to long-term trampling was examined in a system of permanent transects mapped onto the existing trail network of footpaths and rides. Existing trail networks were fieldwalked and mapped during January 1995, which derived the exact location of study transects (Plate 2.1). Eight transects were selected in Tocil and Crackley Woods, and nine in Tilehill Wood. Typical examples of transects at each site are shown in Plates 2.2, 2.3 and 2.4. Transect selection satisfied a number of criteria, namely that trails were:

- surrounded by areas of undisturbed vegetation

Plate 2.2 - Typical fieldwork transect in Tilehill Wood (transect 4 of 9, SP 278 791, November 1995)



Plate 2.3 - Typical fieldwork transect in Crackley Wood (transect 8 of 9, SP 291 738, March 1995)



Plate 2.4 - Typical fieldwork transect in Tocil Wood (transect 7 of 8, SP 305 755, February 1996)



Transect 7 (SP 305 755); Tocil Wood

- regularly exposed to trampling by people and their associated anthropogenic activities
- represented a variety of trail types that included minor and major footpaths, tracks and woodland rides
- showed heterogeneity in environmental conditions such as canopy stratification and soil, vegetation community and sub-community types

Each transect measured 10 m in length and was set up running parallel to the line of wear. Transects were subjectively subdivided into one of four wear classes running perpendicular to the line of wear. The wear classes were proportionally divided into a central heavily trampled zone (H), two adjacent moderately trampled zones (M), two further adjacent lightly trampled zones located on the trail edge (L) and an untrampled control zone present in undisturbed vegetation at least 2 m from the trailside (C). Thus, each transect was divided into six distinct plots. Direct comparison between worn and undisturbed sites helps to detect any differences in vegetation and soil characteristics which are directly attributable to the impact of trampling pressure. By examining results from both individual sites and as a combined mean of all three sites, it was possible to examine general trends in detail. As a consequence, statistical conclusions from the combined site data should be viewed with caution, although conclusions were generally very similar to results liberated in the individual sites.

Four 20 x 20 cm quadrats were randomly placed within each 'wear class' at each transect. Quadrat size was optimally selected using a minimal area method on undisturbed vegetation, and random sampling followed the random walk procedure expressed by Gilbertson *et al.* (1985). Sampling gave 16 quadrats per transect, 128 quadrats per field survey in Tocil and Crackley Woods and 144 quadrats in Tilehill Wood. As a combined total, there were 100 quadrats in each of the four wear classes for each field survey. Field surveys were conducted in four discrete seasonal blocks for each site:

Season	Tocil Wood	Crackley Wood	Tilehill Wood
Spring	April 1995	April 1996	May 1996
Summer	July 1995	August 1996	August 1996
Autumn	October 1995	November 1996	November 1995
Winter	January 1996	February 1996	February 1996

2.2.3 Recording

2.2.3.1 Vegetation and soil parameters

Taxonomic nomenclature of species follows Clapham, Tutin & Warburg (1962) for vascular plants, and Smith (1980) for mosses. Classification according to life-form is illustrated in Fig. 2.1, and is defined by utilising the system developed by Raunkiaer (1934). Individual species strategies are also categorised into one of the ^{seven} ~~many~~ subdivisional classes of the ecological strategy classification developed by Grime *et al.* (1988).

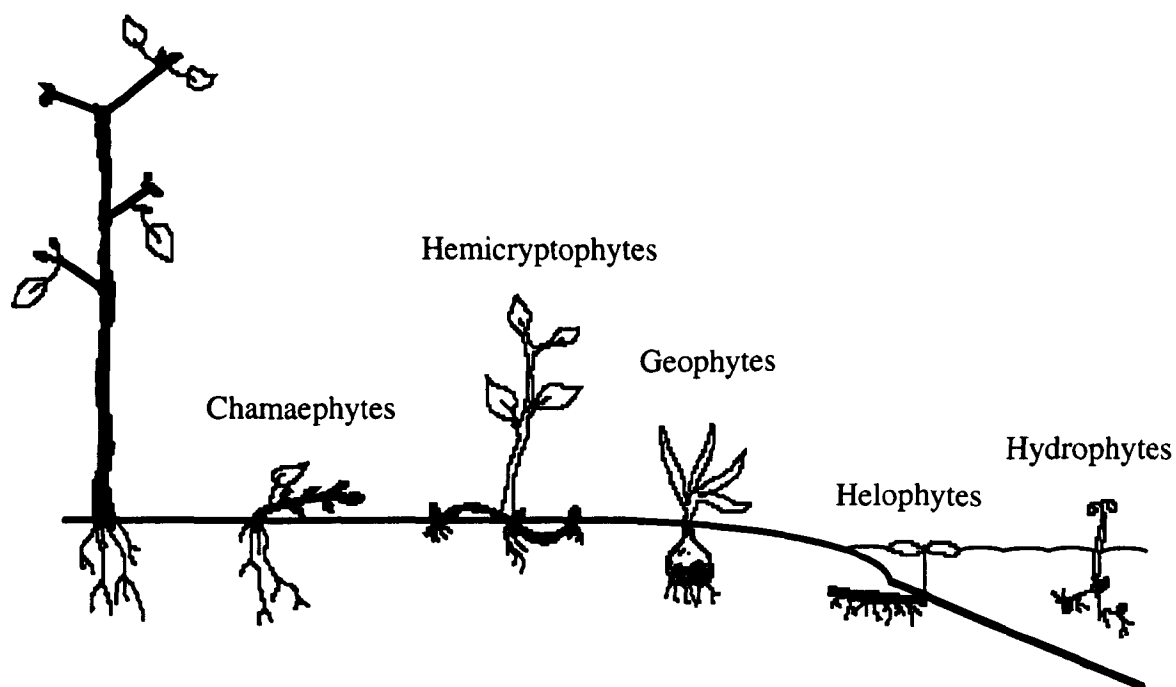
2.2.3.1.1 Total quadrat measurements

The following estimates were made within each quadrat:

- living vascular and bryophyte vegetation cover (%)
- bare ground cover (%)
- leaf litter cover (%)
- leaf litter depth (cm) (expressed as the average depth to the surface organic soil layer at each of the four corners of the quadrat)
- vegetation height (cm) (vegetation height in each of the four corners in each quadrat expressed as a quadrat mean; dead vegetation and the flowering heads of vascular plants were not recorded)
- soil penetrative resistance (average soil penetrative resistance of four random quadrat measurements were estimated by using a hand-held soil

Fig. 2.1 - The major types of life-form. Light lines show plant parts that die in the unfavourable season, whilst heavy lines show the parts that survive and the perennating bud (Raunkiaer 1934).

Phanerophytes



(**Phanerophytes** - woody plants with buds > 25 cm above the soil surface; **chamaephytes** - woody or herbaceous plants with buds above the soil surface but still below 25 cm; **hemicryptophytes** - herbs (rarely woody) with buds at ground level (sub-groups: **protohemicryptophytes** - uniformly leafy stems with basal leaves usually smaller than the rest; **semi-rosette hemicryptophytes** - leafy stems with lower leaves larger than the upper ones, and with shortened basal internodes; **rosette hemicryptophytes** - leafless flowering stems and a basal rosette of leaves); **geophytes** - herbs with buds below the soil surface; **helophytes** - marsh plants; **hydrophytes** - water plants; **therophytes** - plants which pass the unfavourable season as seeds (after Liddle 1997).

penetrometer on surface soils, and expressed in unconfined compressive strength (kg cm^{-2}).

- light intensity (obtained at ground level within each transect as the average of four readings using a hand-held light meter).

2.2.3.1.2 Individual species measurements

Vascular and moss cover (%), maximum height (cm) and morphological parameters of leaf length (cm) and leaf width (cm) were recorded for individual species. The morphological parameters were expressed as a mean of four replicates.

2.2.3.1.3 Soil physical and chemical measurements

Surface soil samples from each quadrat were excavated in each wear class per transect. Wear class samples in each transect were bulked together to reduce variability between measurements (Rowell 1994), and determinations of soil pH, surface soil moisture content ($\text{g H}_2\text{O g}^{-1}$ fresh soil) and soil organic matter content (%) were carried out. The detailed methods for the determination of soil physical and chemical characteristics are described in section 5.2.

2.2.3.2 *Visitor numbers*

Estimates of the annual number of users visiting each woodland each year were made by constructing pressure sensitive counters. These were placed in strategic locations to give accurate frequencies of use for particular groups of transects. Counters worked on a similar principle to those described by Coker & Coker (1972). Each counter consisted of a pressure pad which was connected to a battery powered electromechanical counter housed in a weatherproof plastic box. Once the buried pad was activated by treading, a count was registered on the display dial of the counter which was hidden a few metres away in undisturbed vegetation. Instructions on how to build a pressure sensitive counter, along with an equipment list are given in Appendix 2.1. Sets of counters were monitored for a year in each woodland from January 1995 to January 1996. A preliminary visual calibration experiment showed that approximately 85 % of total passing pedestrian traffic activated the counter.

The lateral distribution of walkers was ascertained by using a 'trampleometer' method (after Bayfield 1971a). Single line transects of fine wire 'pins' were set up in the middle of each transect, running across the trail centre and joining points located 2 m either side of the trail edge and perpendicular to the line of wear at 10 cm intervals. Each 'pin' consisted of a 5 cm oval-headed nail with a 4 cm length of fine copper wire soldered onto the nail head. The 'pins' were inserted flush with the soil surface with the straightened wire projecting vertically in such a way that the passage of walkers

would bend or knock down vertical wires. Wires bent by walkers and other users could then be counted at regular two hour intervals over the course of several daytime field surveys. This enabled the lateral distribution of walkers at each transect to be elucidated, and thus quantified the relative amount of use that occurred within each wear class.

By combining these data a rough estimation of the total and seasonal number of visitors in each wood, and ultimately each wear class, was possible.

2.2.4 Statistical analysis

Statistical analysis was performed using SYSTAT 5.2.1, StatView II and Multi Variate Statistical Package (MVSP) *Plus* Ver. 2.2.

2.2.4.1 Preliminary tests

Kruskal-Wallis single factor analysis of variance tests were used to test for significant differences between wear classes in environmental variables and species data in sites and seasons. Spearman rank correlations were used to examine the strength of relationships amongst the environmental parameters. Some environmental variables were data transformed in each season in order to conform to the assumptions of homoscedasticity and normality (Zar 1984). Partial correlation matrices with multiple correlations and multiple stepwise regression models were then applied to the transformed environmental variable data.

Species diversity indices configured for each quadrat location in the spring and summer surveys used the Shannon diversity index ' H ' (Begon *et al.* 1990):

$$H = - \sum_{i=1}^s (P_i)(\log_2 P_i)$$

where ' H ' was the index number, ' s ' was the total number of species, ' P_i ' was the importance value of a given species ' i ', and ' $(\log_2 P_i)$ ' was log to the base 2 of that importance value.

2.2.4.2 Ordination analyses

Trampling is assumed to be the major external factor controlling species abundance, so it was necessary to develop a measure of how well trampling explained the species data. The chosen ordination techniques of correspondence analysis (CA) and detrended correspondence analysis (DCA) developed by Hill & Gauch (1980) constructed the theoretical variable that best explained the species data. Hence, species and site ordination axes were extracted from the species data alone. The procedure generates eigenvalues, which are equivalent to the (maximised) dispersion of species scores on each ordination axis, and thus act as a measure of importance (Jongman *et al.* 1995). This method offered an effective approximate solution in the ordination problem for a unimodal response model in two or more dimensions (Jongman *et al.* 1995).

Species percent cover values were converted using the ten point abundance class octave scale available in the M.V.S.P *Plus* Ver. 2.2 program. Commonly used in plant community ecology, the scale is roughly based on log₂ (Gauch 1982). Data were converted to classes based on the following scale:

Percent cover	Octave scale
0	0
> 0 - 0.5	1
> 0.5 - 1	2
> 1 - 2	3
> 2 - 4	4
> 4 - 8	5
> 8 - 16	6
> 16 - 32	7
> 32 - 64	8
> 64 - 100	9

A reciprocal averaging method as described by Hill (1978) was utilised as the detrending algorithm for DCA. As the ordination is sensitive to species that occurred in a few 'species poor sites', rare species were downweighted before the analysis to

reduce their overall influence. Finally, relationships of the first two DCA axes with environmental variables were investigated by ranked correlations and multiple regression analysis in both the spring and summer surveys.

2.3 Results

2.3.1 *Seasonal changes in environmental parameters*

2.3.1.1 *Vegetation cover*

Vegetation cover at each of the three sites decreases significantly as trampling intensity increases (Appendices 2.2, 2.3, 2.4 and 2.5). Cover reaches a maximum in summer, and falls to a minimum in winter in all four wear classes, with little difference between lightly trampled and undisturbed areas (Fig. 2.2a). Amongst the different plant groups, the proportional cover of graminoid and moss species is higher in heavily and moderately trampled areas compared to lightly trampled and undisturbed areas, where vascular plants predominate, e.g.: in summer vegetation is composed of 60 % graminoids and 18 % mosses in heavily trampled path centres, compared to just 11 % graminoids and 2 % mosses off-trail in undisturbed areas.

Many of the correlations involving vegetation cover are statistically significant, with recurrent trends representative across all four seasons, but the greatest number of significant differences occur during summer (Table 2.2a, 2.3a, 2.4a and 2.5a). For instance, there are positive significant correlations with leaf litter depth, litter cover and vegetation height, and negative significant correlations with bare ground, soil penetrative resistance, soil pH and visitor numbers. As simple correlations between variables may be obscured by additional factors, the partial correlation matrices clarify complex inter-relationships amongst variables (Table 2.2b, 2.3b, 2.4b and 2.5b). Vegetation cover retains a significant negative correlation with visitor numbers in summer and autumn, and remains positively correlated with bare ground cover, leaf litter cover and vegetation height throughout all four seasons. The squared multiple correlations are all high, indicating that variation in vegetation cover of up to 93 % (in spring) can be predicted, in a linear sense, from the other ten variables.

Multiple stepwise regressions of all the environmental variables on vegetation cover shows that the best single predictors are bare ground cover in winter and spring,

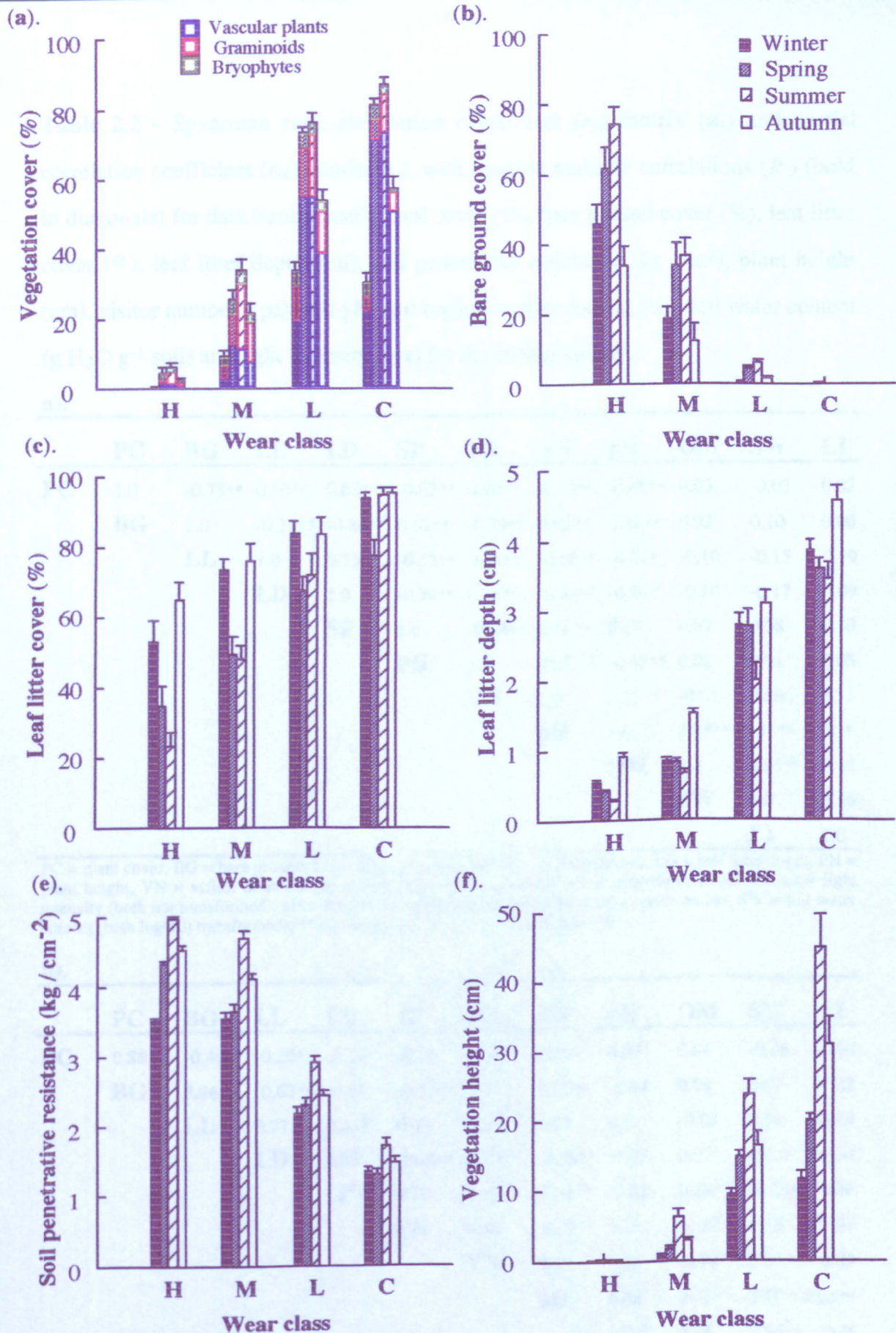


Fig. 2.2 - Total vegetation cover (a), total bare ground cover (b), total leaf litter cover (c), leaf litter depth (d), soil penetrative resistance (e) and vegetation height (f) as a quadrat mean for all sites in the four wear classes in winter, spring, summer and autumn (H, heavily trampled; M, moderately trampled; L, lightly trampled; C, control).

Table 2.2 - Spearman rank correlation coefficient (r_s) matrix (**a.**) and partial correlation coefficient (r_{ik}) matrix (**b.**), with squared multiple correlations (R) (bold in diagonals) for data transformed: plant cover (%), bare ground cover (%), leaf litter cover (%), leaf litter depth (cm), soil penetrative resistance (kg cm⁻²), plant height (cm), visitor numbers (pa), soil pH, soil organic matter content (%), soil water content (g H₂O g⁻¹ soil) and light intensity (lux) for the **winter** survey.

a).

	PC	BG	LL	LD	SP	PH	VN	pH	OM	SW	LI
PC	1.0	-0.78**	0.40**	0.68**	-0.62**	0.90**	-0.71**	-0.40**	0.03	-0.03	0.02
BG		1.0	-0.71**	-0.84**	0.67**	-0.79**	0.83**	0.37**	0.02	0.10	0.06
LL			1.0	0.75**	-0.53**	0.46**	-0.66**	-0.21*	-0.10	-0.15	-0.19
LD				1.0	-0.79**	0.76**	-0.88**	-0.24*	-0.10	-0.17	-0.09
SP					1.0	-0.68**	0.78**	0.17	0.07	0.08	0.10
PH						1.0	-0.77**	-0.42**	0.08	0.01	0.05
VN							1.0	0.32**	-0.01	0.08	0.11
pH								1.0	-0.45**	-0.38**	-0.21*
OM									1.0	0.95**	0.15
SW										1.0	0.16
LI											1.0

PC = plant cover, BG = bare ground, LL = leaf litter cover (all arcsine transformed); LD = leaf litter depth, PH = plant height, VN = visitor numbers (all square root transformed); SP = soil penetrative resistance, LI = light intensity (both not transformed); pH = soil pH (inverse transformed); OM = soil organic matter, SW = soil water content (both log(10) transformed); ** sig. at $p \leq 0.01$; * sig. at $p \leq 0.05$; $n = 100$

b).

	PC	BG	LL	LD	SP	PH	VN	pH	OM	SW	LI
PC	0.85	-0.40**	-0.26*	-0.18	-0.18	0.69**	0.01	0.09	0.04	-0.08	-0.04
BG		0.86	-0.62**	-0.05	-0.33**	0.04	0.37**	-0.04	0.08	0.07	-0.02
LL			0.77	0.35*	0.01	-0.10	0.07	0.11	-0.09	0.09	-0.19
LD				0.89	-0.42**	0.36**	-0.36**	-0.05	0.07	-0.13	0.09
SP					0.72	0.03	0.30**	-0.01	0.28**	-0.29**	0.09
PH						0.88	-0.11	0.10	-0.12	0.18	0.07
VN							0.87	0.06	-0.33**	0.31**	0.05
pH								0.48	0.43**	-0.31**	0.28**
OM									0.94	0.95**	-0.16
SW										0.93	0.16
LI											0.18

** sig. at $p \leq 0.01$; * sig. at $p \leq 0.05$; $n = 100$

Table 2.3 - Spearman rank correlation coefficient (r_s) matrix (**a.**) and partial correlation coefficient (r_{ik}) matrix (**b.**), with squared multiple correlations (R) (bold in diagonals) for data transformed: plant cover (%), bare ground cover (%), leaf litter cover (%), leaf litter depth (cm), soil penetrative resistance (kg cm⁻²), plant height (cm), visitor numbers (pa), soil pH, soil organic matter content (%), soil water content (g H₂O g⁻¹ soil) and light intensity (lux) for the **spring** survey.

a).

	PC	BG	LL	LD	SP	PH	VN	pH	OM	SW	LI
PC	1.0	-0.78**	0.43**	0.82**	-0.85**	0.90**	-0.86**	-0.29**	0.12	0.15	-0.05
BG		1.0	-0.71**	-0.86**	0.76**	-0.80**	0.83**	0.32**	-0.14	-0.29**	0.10
LL			1.0	0.49**	-0.45**	0.62**	-0.53**	-0.41**	0.15	0.25*	-0.01
LD				1.0	-0.86**	0.80**	-0.88**	-0.19	0.07	0.19	-0.20
SP					1.0	-0.87**	0.91**	0.20*	-0.14	-0.19	0.13
PH						1.0	-0.87**	-0.41**	0.19	0.16	0.02
VN							1.0	0.27**	-0.11	-0.17	0.15
pH								1.0	-0.39**	-0.28**	-0.16
OM									1.0	0.81**	0.13
SW										1.0	-0.03
LI											1.0

PC = plant cover, BG = bare ground, LL = leaf litter cover (all arcsine transformed); LD = leaf litter depth, PH = plant height, VN = visitor numbers, OM = organic matter (all square root transformed); SP = soil penetrative resistance, pH = soil pH, SW = soil water content (all not transformed); LI = light intensity (log(10) transformed); ** sig. at $p \leq 0.01$; * sig. at $p \leq 0.05$; $n = 100$

b).

	PC	BG	LL	LD	SP	PH	VN	pH	OM	SW	LI
PC	0.93	-0.47**	-0.56**	-0.28**	-0.15	0.66**	-0.12	-0.03	-0.11	0.04	0.04
BG		0.92	-0.73**	-0.56**	-0.25*	0.35**	0.30**	-0.07	0.11	-0.23*	-0.01
LL			0.78	-0.46**	-0.07	0.56**	0.07	-0.16	-0.10	0.04	-0.02
LD				0.88	-0.28**	0.37**	-0.07	0.02	-0.08	0.02	-0.16
SP					0.89	-0.16	0.45**	-0.18	0.04	-0.14	0.07
PH						0.94	-0.15	-0.13	0.29**	-0.23**	0.13
VN							0.92	0.07	0.01	0.08	0.05
pH								0.30	-0.18	0.06	-0.08
OM									0.74	0.83**	0.13
SW										0.74	-0.12
LI											0.17

** sig. at $p \leq 0.01$; * sig. at $p \leq 0.05$; $n = 100$

Table 2.4 - Spearman rank correlation coefficient (r_s) matrix (**a.**) and partial correlation coefficient (r_{ik}) matrix (**b.**), with squared multiple correlations (R) (bold in diagonals) for data transformed: plant cover (%), bare ground cover (%), leaf litter cover (%), leaf litter depth (cm), soil penetrative resistance (kg cm⁻²), plant height (cm), visitor numbers (pa), soil pH, soil organic matter content (%), soil water content (g H₂O g⁻¹ soil) and light intensity (lux) for the **summer** survey.

a).

	PC	BG	LL	LD	SP	PH	VN	pH	OM	SW	LI
PC	1.0	-0.79**	0.60**	0.71**	-0.79**	0.89**	-0.77**	-0.43**	0.54**	0.36**	-0.23*
BG		1.0	-0.86**	-0.88**	0.87**	-0.84**	0.84**	0.34**	-0.41**	-0.32**	0.32*
LL			1.0	0.85**	-0.80**	0.72**	-0.80**	-0.27**	0.29**	0.16	-0.35*
LD				1.0	-0.87**	0.80**	-0.86**	-0.19	0.30**	0.16	-0.36*
SP					1.0	-0.88**	0.84**	0.42**	-0.54**	-0.35**	0.29*
PH						1.0	-0.82**	-0.40**	0.57**	0.39*	-0.25*
VN							1.0	0.31**	-0.42**	-0.27**	0.41**
pH								1.0	-0.50**	-0.58**	0.07
OM									1.0	0.64**	0.02
SW										1.0	-0.11
LI											1.0

PC = plant cover, BG = bare ground, LL = leaf litter cover (all arcsine transformed); OM = soil organic matter, PH = plant height, VN = visitor numbers (all square root transformed); SP = soil penetrative resistance, LI = light intensity, pH = soil pH (all not transformed); LD = leaf litter depth, SW = soil water content (both log(10) transformed); ** sig. at $p \leq 0.01$; * sig. at $p \leq 0.05$; $n = 100$

b).

	PC	BG	LL	LD	SP	PH	VN	pH	OM	SW	LI
PC	0.88	-0.57**	-0.46**	-0.24*	0.04	0.65**	-0.32**	-0.18	-0.03	-0.12	0.12
BG		0.90	-0.50**	-0.46**	0.01	0.26*	-0.01	-0.10	0.03	-0.19	-0.01
LL			0.82	0.08	-0.14	0.29**	-0.16	-0.17	-0.03	-0.21*	-0.02
LD				0.87	-0.21*	0.20	-0.30**	0.14	-0.16	-0.04	-0.04
SP					0.86	-0.34**	0.23*	0.22*	-0.18	-0.01	0.03
PH						0.89	0.13	0.11	0.20	0.08	-0.03
VN							0.84	-0.08	-0.09	0.02	0.20
pH								0.44	-0.07	-0.38**	0.08
OM									0.59	0.43**	0.21*
SW										0.52	-0.10
LI											0.22

** sig. at $p \leq 0.01$; * sig. at $p \leq 0.05$; $n = 100$

Table 2.5 - Spearman rank correlation coefficient (r_s) matrix (**a.**) and partial correlation coefficient (r_{ik}) matrix (**b.**), with squared multiple correlations (R) (bold in diagonals) for data transformed: plant cover (%), bare ground cover (%), leaf litter cover (%), leaf litter depth (cm), soil penetrative resistance (kg cm⁻²), plant height (cm), visitor numbers (pa), soil pH, soil organic matter content (%), soil water content (g H₂O g⁻¹ soil) and light intensity (lux) for the **autumn** survey.

a).

	PC	BG	LL	LD	SP	PH	VN	pH	OM	SW	LI
PC	1.0	-0.63**	0.30**	0.65**	-0.75**	0.92**	-0.76**	-0.23*	0.21*	0.08	-0.01
BG		1.0	-0.77**	-0.76**	0.74**	-0.74**	0.70**	0.38**	-0.23*	-0.23*	-0.05
LL			1.0	0.70**	-0.58**	0.49**	-0.57**	-0.30**	0.14	0.18	0.01
LD				1.0	-0.80**	0.78**	-0.80**	-0.21*	0.15	0.06	-0.03
SP					1.0	-0.85**	0.77**	0.38**	-0.35**	-0.34**	-0.03
PH						1.0	-0.81**	-0.29**	0.27**	0.18	0.03
VN							1.0	0.17	-0.06	-0.01	0.22*
pH								1.0	-0.73**	-0.64**	-0.21*
OM									1.0	0.81**	0.15
SW										1.0	0.23*
LI											1.0

PC = plant cover, BG = bare ground, LL = leaf litter cover (all arcsine transformed); SW = soil water content, PH = plant height, VN = visitor numbers (all square root transformed); SP = soil penetrative resistance, pH = soil pH, LI = light intensity (all not transformed); LD = leaf litter depth, OM = soil organic matter, (both log(10) transformed); ** sig. at $p \leq 0.01$; * sig. at $p \leq 0.05$; $n = 100$

b).

	PC	BG	LL	LD	SP	PH	VN	pH	OM	SW	LI
PC	0.89	-0.54**	-0.63**	-0.04	-0.18	0.60**	-0.25*	0.01	0.13	-0.20	0.09
BG		0.82	-0.71**	-0.01	-0.03	0.23*	0.05	0.13	0.16	-0.18	0.01
LL			0.80	0.29**	-0.15	0.23*	-0.09	-0.02	-0.01	-0.02	0.02
LD				0.77	-0.19	0.21*	-0.25*	0.05	0.13	-0.22*	0.07
SP					0.80	-0.17	0.21*	0.07	0.06	-0.26*	-0.02
PH						0.87	-0.12	0.12	0.06	0.12	0.11
VN							0.82	0.07	0.06	0.15	0.34**
pH								0.56	-0.45**	-0.04	-0.20
OM									0.77	0.69**	-0.23*
SW										0.76	0.21*
LI											0.26

** sig. at $p \leq 0.01$; * sig. at $p \leq 0.05$; $n = 100$

vegetation height in summer and soil penetrative resistance in autumn (Table 2.6, 2.7, 2.8 and 2.9). The highest variance in vegetation cover is explained by vegetation height in the summer survey ($r^2 = 0.78$), and in all four seasonal models vegetation height, leaf litter cover and bare ground cover significantly contribute to the model.

2.3.1.2 *Bare ground cover*

Bare ground cover increases significantly as the amount of trampling intensifies in all four seasons, so the extent of bare ground exposure is related to the level of wear (Appendices 2.2, 2.3, 2.4 and 2.5). For instance, the amount of bare ground on path surfaces in heavily trampled trail centres during summer is approximately twofold greater than in autumn, but differences in bare ground cover between lightly trampled and undisturbed areas are minimal (Fig. 2.2b).

The amount of bare ground cover is positively correlated with soil penetrative resistance, visitor numbers and soil pH, and negatively correlated with vegetation cover and height and leaf litter cover and depth (Table 2.2a, 2.3a, 2.4a and 2.5a). Partial correlations with leaf litter cover and depth remain highly negative and significant in spring and summer, and there remains positive significant partial correlations with visitor numbers in winter and spring (Table 2.2b, 2.3b, 2.4b and 2.5b).

The best single predictor of bare ground cover is vegetation cover in winter and spring, litter depth in summer and litter cover in autumn (Table 2.6, 2.7, 2.8 and 2.9). In common with all four seasonal models, significant contributions are made to each model by vegetation cover and litter cover.

2.3.1.3 *Leaf litter cover*

Leaf litter cover significantly decreases as trampling intensity increases in all four seasons (Appendices 2.2, 2.3, 2.4 and 2.5). Litter cover is approximately 100 % in undisturbed areas in summer, autumn and winter, but plummets to a minimum of 23

Table 2.6 - Multiple stepwise regression models (forward selective) generated for transformed environmental dependent variables (DV), with best single predictor (BP) for the **winter** data

DV ^a	BP	r ²	Stepwise model	r ²	F ^b
PC	BG	0.51	$Y' = 26.2 - 0.29BG - 0.21LL + 2.39PH$	0.84	177.5***
BG	PC	0.51	$Y' = 63.7 - 0.52PC - 0.56LL - 3.98SP + 0.49VN$	0.86	147.7***
LL	BG	0.65	$Y' = 77.1 - 0.52PC - 0.70BG + 4.17LD - 0.001LI$	0.76	79.6***
LD	BG	0.63	$Y' = 3.83 - 0.02PC + 0.02LL - 0.39SP + 0.13PH - 0.04VN - 1.06SW$	0.89	124.2***
SP	LD	0.61	$Y' = 4.70 - 0.02PC - 0.02BG - 0.44LD + 0.03VN$	0.69	52.2***
PH	PC	0.81	$Y' = -0.40 + 0.20PC - 0.02LL + 1.05LD + 3.71SW$	0.87	167.7***
VN	PC	0.53	$Y' = 81.9 + 0.23BG - 3.28LD + 3.02SP - 0.37PH - 25.0OM + 50.1SW$	0.87	102.9***
pH	OM	0.22	$Y' = -0.06 + 0.001PC + 0.12OM - 0.17SW + 0.00001LI$	0.45	20.6***
OM	SW	0.90	$Y' = 1.87 + 0.001BG + 0.03SP - 0.004VN + 1.39pH + 1.93SW - 0.001LI$	0.94	226.2***
SW	OM	0.90	$Y' = -0.96 - 0.01SP + 0.002PH + 0.002VN - 0.45pH + 0.47OM$	0.93	242.3***
LI	pH	0.07	$Y' = 3595.6 - 15.9LL + 13378.8pH$	0.13	7.7***

^a - PC = plant cover, BG = bare ground, LL = leaf litter cover (all arcsine transformed); LD = leaf litter depth, PH = plant height, VN = visitor numbers (all square root transformed); SP = soil penetrative resistance, LI = light intensity (both not transformed); pH = soil pH (inverse transformed); OM = soil organic matter, SW = soil water content (both log(10) transformed).

^b - *** sig. at $p \leq 0.001$; ** sig. at $p \leq 0.01$; * sig. at $p \leq 0.05$; $n = 100$

Table 2.7 - Multiple stepwise regression models (forward selective) generated for transformed environmental dependent variables (DV), with best single predictor (BP) for the **spring** data

DV ^a	BP	r ²	Stepwise model	r ²	F ^b
PC	BG	0.65	$Y' = 68.6 - 0.48BG - 0.37LL - 2.9LD - 3.12SP + 3.53PH - 0.6OM$	0.92	192.1***
BG	PC	0.65	$Y' = 86.3 - 0.53PC - 0.51LL - 6.55LD - 3.73SP + 2.25PH + 0.47VN - 12.4SW$	0.91	140.2***
LL	BG	0.55	$Y' = 108.7 - 0.88PC - 1.06BG - 7.44LD + 4.46PH$	0.77	82.1***
LD	PC	0.70	$Y' = 12.7 - 0.02PC - 0.05BG - 0.03LL - 0.46SP + 0.17PH - 1.81LI$	0.88	113.3***
SP	PC	0.78	$Y' = 4.3 - 0.01BG - 0.18LD - 0.07PH + 0.05VN - 0.15pH - 0.60SW$	0.88	118.8***
PH	PC	0.86	$Y' = -3.4 + 0.14PC + 0.06BG + 0.07LL + 0.77LD - 0.67SP - 0.35pH + 0.45OM - 4.7SW$	0.94	180.6***
VN	PC	0.82	$Y' = 10.5 - 0.11PC + 0.19BG + 5.11SP - 0.45PH + 5.21SW$	0.91	202.7***
pH	LL	0.13	$Y' = 5.6 - 0.01LL - 0.20OM + 1.47SW$	0.23	9.7***
OM	SW	0.63	$Y' = -4.8 + 0.02BG + 0.11PH - 0.31pH + 10.05SW + 2.23LI$	0.73	50.8***
SW	OM	0.63	$Y' = 0.3 - 0.002BG - 0.02SP - 0.02PH + 0.07OM$	0.73	63.6***
LI	LD	0.04	$Y' = 2.8 - 0.03LD + 0.007PH$	0.13	7.14**

^a - PC = plant cover, BG = bare ground, LL = leaf litter cover (all arcsine transformed); LD = leaf litter depth, PH = plant height, VN = visitor numbers, OM = organic matter (all square root transformed); SP = soil penetrative resistance, pH = soil pH, SW = soil water content (all not transformed); LI = light intensity (log(10) transformed).

b - *** sig. at $p \leq 0.001$; ** sig. at $p \leq 0.01$; * sig. at $p \leq 0.05$; $n = 100$

Table 2.8 - Multiple stepwise regression models (forward selective) generated for transformed environmental dependent variables (DV), with best single predictor (BP) for the **summer** data

DV ^a	BP	r ²	Stepwise model	r ²	F ^b
PC	PH	0.78	$Y' = 52.3 - 0.54BG - 0.35LL + 2.30PH$	0.85	186.0***
BG	LD	0.79	$Y' = 79.9 - 0.51PC - 0.36LL - 19.73LD + 0.70PH$	0.90	210.6***
LL	BG	0.71	$Y' = 94.7 - 0.61PC - 0.64BG + 1.56PH - 0.56VN$	0.78	84.1***
LD	BG	0.79	$Y' = 1.7 - 0.01PC - 0.01BG + 0.02PH - 0.01VN$	0.85	137.3***
SP	PH	0.76	$Y' = 2.7 - 0.71LD - 0.07PH + 0.02VN + 0.38pH$	0.85	136.3***
PH	PC	0.78	$Y' = -3.2 + 0.18PC + 0.09BG + 0.06LL + 2.63LD - 1.61SP + 0.67OM$	0.88	118.1***
VN	PC	0.79	$Y' = 34.6 - 0.18PC - 0.08LL - 10.34LD + 2.37SP + 0.0005LI$	0.83	94.1***
pH	SW	0.32	$Y' = 2.9 + 0.33LD + 0.21SP - 1.13SW$	0.41	22.1***
OM	SW	0.40	$Y' = 5.9 + 0.07PH + 3.30SW + 0.0001LI$	0.55	38.7***
SW	OM	0.40	$Y' = -0.38 - 0.13pH + 0.07OM$	0.49	46.2***
LI	VN	0.14	$Y' = 2412.0 + 76.8VN + 392.8OM$	0.18	10.9***

^a - PC = plant cover, BG = bare ground, LL = leaf litter cover (all arcsine transformed); OM = soil organic matter, PH = plant height, VN = visitor numbers (all square root transformed); SP = soil penetrative resistance, LI = light intensity, pH = soil pH (all not transformed); LD = leaf litter depth, SW = soil water content (both log(10) transformed).

^b - *** sig. at $p \leq 0.001$; ** sig. at $p \leq 0.01$; * sig. at $p \leq 0.05$; $n = 100$

Table 2.9 - Multiple stepwise regression models (forward selective) generated for transformed environmental dependent variables (DV), with best single predictor (BP) for the **autumn** data

DV ^a	BP	r ²	Stepwise model	r ²	F ^b
PC	SP	0.58	$Y' = 67.2 - 0.51BG - 0.51LL + 1.71PH - 0.30VN$	0.88	167.7***
BG	LL	0.59	$Y' = 77.2 - 0.60PC - 0.64LL + 0.66PH - 8.74SW$	0.82	102.0***
LL	BG	0.59	$Y' = 79.6 - 0.75PC - 0.84BG + 17.47LD - 0.31SP + 0.73PH$	0.80	72.0***
LD	BG	0.51	$Y' = 0.93 + 0.01LL + 0.01PH - 0.01VN$	0.76	94.8***
SP	PC	0.58	$Y' = 33.1 - 0.10PC - 0.07LL - 4.49LD - 0.25PH + 0.12VN - 13.06SW$	0.80	58.4***
PH	PC	0.77	$Y' = -4.89 + 0.20PC + 5.07LD - 0.15SP + 3.49SW$	0.85	130.2***
VN	PC	0.61	$Y' = 34.0 - 0.34PC - 0.13LL - 11.50LD + 0.42SP + 15.12SW + 0.002LI$	0.82	65.9***
pH	OM	0.49	$Y' = 6.9 + 0.01BG + 0.01PH - 1.54OM - 0.0001LI$	0.55	28.4***
OM	SW	0.76	$Y' = 1.22 + 0.003PC + 0.002BG - 0.14pH + 1.32SW - 0.00002LI$	0.76	58.4***
SW	OM	0.66	$Y' = 0.27 - 0.002PC - 0.001BG - 0.11LD - 0.004SP + 0.37OM + 0.00001LI$	0.75	44.1***
LI	SW	0.10	$Y' = 8001.2 + 107.7PH + 54.54VN - 665.8pH - 2261.0OM + 3895.6SW$	0.24	5.8***

^a - PC = plant cover, BG = bare ground, LL = leaf litter cover (all arcsine transformed); SW = soil water content, PH = plant height, VN = visitor numbers (all square root transformed); SP = soil penetrative resistance, pH = soil pH, LI = light intensity (all not transformed); LD = leaf litter depth, OM = soil organic matter, (both log(10) transformed).

^b - *** sig. at $p \leq 0.001$; ** sig. at $p \leq 0.01$; * sig. at $p \leq 0.05$; $n = 100$

% in heavily trampled paths in summer. The amount of litter cover is highest in autumn and winter and lowest in summer and spring (Fig. 2.2c).

There are significant positive correlations with vegetation cover, litter depth and vegetation height, and significant negative correlations with bare ground cover, soil penetrative resistance, soil pH and visitor numbers (Table 2.2a, 2.3a, 2.4a and 2.5a). Partial correlations with the indicators of trampling intensity, (visitor numbers and soil penetrative resistance) are not significant across the seasonal range, but squared multiple correlations remain high (Table 2.2b, 2.3b, 2.4b and 2.5b).

In all four seasons, the best single predictor of litter cover is bare ground cover, with the highest coefficient of determination during summer ($r^2 = 0.71$) (Table 2.6, 2.7, 2.8 and 2.9). There are significant contributions to stepwise models by vegetation cover and bare ground cover in all four seasons, by vegetation height in all except the winter survey and by visitor numbers in the spring and summer surveys.

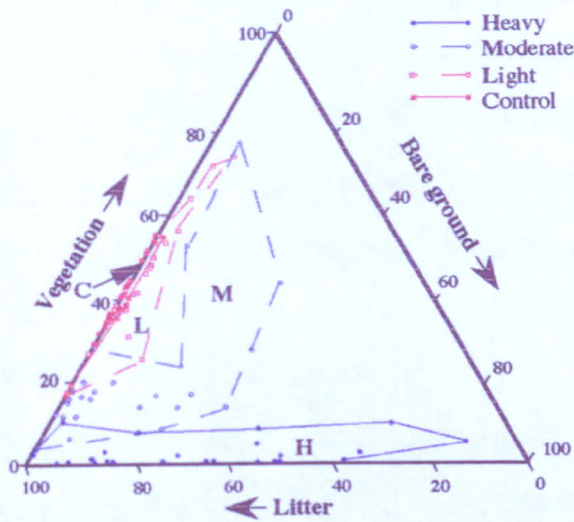
2.3.1.4 *Inter-relationships between primary cover attributes*

The relative proportions of the three primary cover attributes of vegetation cover, bare ground cover and leaf litter cover are plotted together for separate autumn, winter, spring and summer surveys on triangular graphs (Fig. 2.3a, 2.3b, 2.3c and 2.3d respectively). Wear classes are aggregated in localised or widespread clusters, indicating that directional changes in primary cover attributes are primarily influenced by trampling and the effects of seasonality.

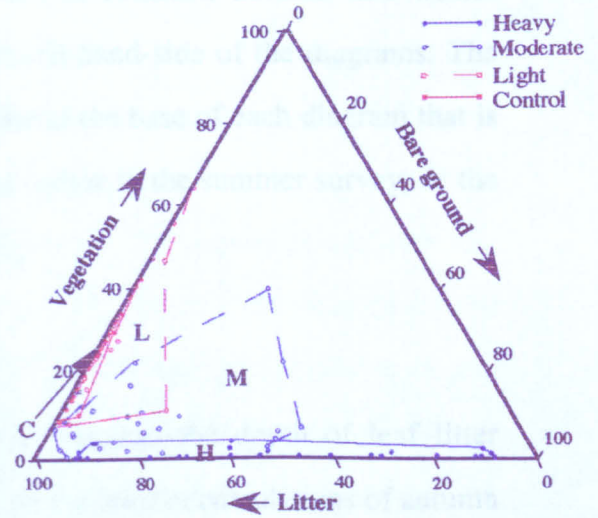
In general, control and lightly trampled wear classes are restricted to a zone on the left hand side of each diagram. During periods of peak visitor pressure and vegetation productivity in summer and spring, the lightly trampled wear classes aggregate outwards and towards the top left handside of the diagrams. During winter and autumn, when vegetation productivity and visitor pressure are lower, wear classes aggregate in the bottom left hand corner of the diagrams.

The moderate wear class zone typifies intermediate levels of disturbance, with approximately equal levels of each primary cover attribute. Clustering is widespread

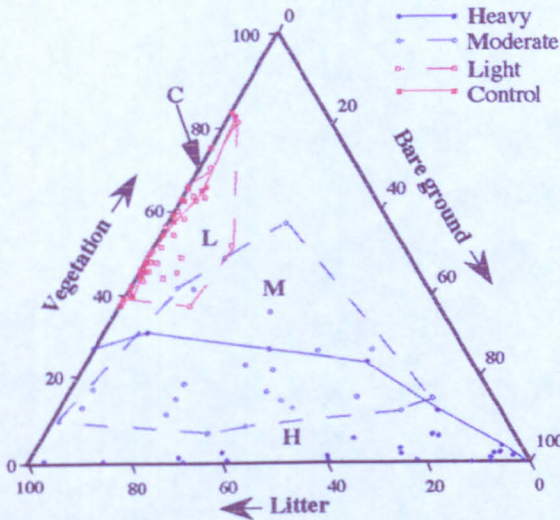
a. Autumn



b. Winter



c. Spring



d. Summer

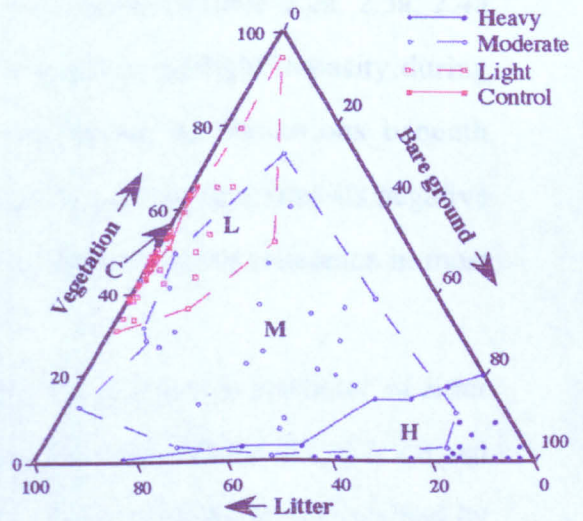


Fig. 2.3 - Relative proportions of the three primary cover attributes of total vegetation cover (%), total bare ground cover (%) and total leaf litter cover (%) during autumn (**a.**), winter (**b.**), spring (**c.**) and summer (**d.**) in each of the four wear classes.

and extends to the right handside of the diagrams in the seasons of summer and spring, which are exposed to peak visitor use. In contrast, autumn and winter clustering is conspicuously concentrated in the left hand-side of the diagrams. The final heavily trampled wear class occupies a zone at the base of each diagram that is generally concentrated in the bottom right hand corner in the summer survey, or the bottom left hand corner in the remaining seasons.

2.3.1.5 *Leaf litter depth*

The physical impact of trampling significantly reduces the depth of leaf litter (Appendices 2.2, 2.3, 2.4 and 2.5), declining from the thick accumulations of autumn to the thin layers of summer across the range of wear classes (Fig. 2.2d).

There are highly significant positive correlations over the four seasons with vegetation cover, litter cover and vegetation height, and negative correlations with bare ground, soil penetrative resistance and visitor numbers (Table 2.2a, 2.3a, 2.4a and 2.5a). The relationships with organic matter content and light intensity during summer verifies that litter depths persist at far deeper accumulations beneath undisturbed vegetation compared to trampled paths. Litter depth retains its negative significant relationships with visitor numbers and soil penetrative resistance in most seasons (Table 2.2b, 2.3b, 2.4b and 2.5b).

During the winter, summer and autumn surveys the best single predictor of litter depth is bare ground cover, and in spring it is vegetation cover (Table 2.6, 2.7, 2.8 and 2.9). Additionally, the highest proportion of variance in litter depth is explained by bare ground cover in the summer survey ($r^2 = 0.79$), and vegetation height is the only significant variable common to all four models.

2.3.1.6 *Soil penetrative resistance*

Levels of soil compaction fall from trampled soils to undisturbed soils off-trail (Appendices 2.2, 2.3, 2.4 and 2.5). The trend of soils that suffer from severe compaction in summer and soils where compaction is less severe in winter

corresponds with seasonal fluctuations in visitor use patterns (Fig. 2.2e). Heavily, moderately and lightly compacted soils are approximately 3.1, 2.8 and 1.7 times more compact than undisturbed soils during spring, summer and autumn. In addition, in Tilehill and Crackley Woods, moderately trampled soils are marginally more compact than the heavily trampled soils in winter.

There are significant positive relationships with bare ground and visitor numbers, and significant negative relationships with vegetation height and cover, litter cover and depth in all seasons (Table 2.2a, 2.3a, 2.4a and 2.5a). The continual use of soil penetrative resistance as a reliable surrogate measure of trampling intensity is validated by virtue of the partial correlations with visitor numbers remaining positive and significant all year round (Table 2.2b, 2.3b, 2.4b and 2.5b). A positive significant partial correlation with soil pH is also recorded in the summer survey. ~~Interesting~~ ^SSignificant negative partial correlations are recorded with soil water in winter and autumn, and with vegetation height in the summer survey.

The best single predictors of soil penetrative resistance are identified as vegetation cover in spring and autumn, litter depth in winter and vegetation height in summer (Table 2.6, 2.7, 2.8 and 2.9). In common with all four seasons, visitor numbers and litter depth both contribute significantly to the models, as does vegetation height in all seasonal surveys with the exception of winter.

2.3.1.7 *Vegetation height*

Vegetation height decreases rapidly with increasing levels of trampling, with tall vegetation conspicuously absent from areas that receive heavy and moderate trampling (Appendices 2.2, 2.3, 2.4 and 2.5). Height differs significantly between sites in lightly and control trampled wear class zones, with low levels of trampling reducing vegetation height by up to half when compared with undisturbed vegetation in summer. The tallest vegetation occurs grows in summer, followed by autumn, then spring to the shortest vegetation in winter. Indeed, the vegetation height of

undisturbed vegetation during summer shows that vegetation is approximately four times taller than stands in winter (Fig. 2.2f).

There are significant negative correlations with bare ground cover, visitor numbers and soil penetrative resistance, and positive significant relationships with vegetation cover, litter cover and depth in all seasons (Table 2.2a, 2.3a, 2.4a and 2.5a). Significant positive correlations are also recorded with organic matter and soil water content in summer and autumn. There are positive significant partial correlations with litter cover in spring and with litter depth all year round, indicating that the tallest plants tend to produce the most litter (Table 2.2b, 2.3b, 2.4b and 2.5b).

Vegetation cover is revealed as the best single predictor of vegetation height in all four seasons, with the highest coefficient of determination in the spring survey ($r^2 = 0.86$) (Table 2.6, 2.7, 2.8 and 2.9). In all four seasons, both vegetation cover and litter depth make significant contributions to the models, as does soil penetrative resistance in all seasons except winter, and soil water content in all seasons except summer.

2.3.1.8 *Visitor numbers*

Visitors use is concentrated along trail centres in all four seasons (Fig. 2.4a), with visitor numbers declining with increasing distance from the path centre and falling to a negligible amount off-trail (Appendices 2.2, 2.3, 2.4 and 2.5). Heavily trampled path centres receive fifty-two times the amount of pedestrian traffic encountered in control zones, six times that found in lightly trampled zones and approximately twice that of moderately trampled areas (Table 2.10).

The visitor counts indicate that Tilehill and Crackley Woodlands are used by double the amount of visitors compared to Tocil Wood. As a consequence, visitor numbers recorded in heavily and moderately trampled wear classes differ statistically between sites.

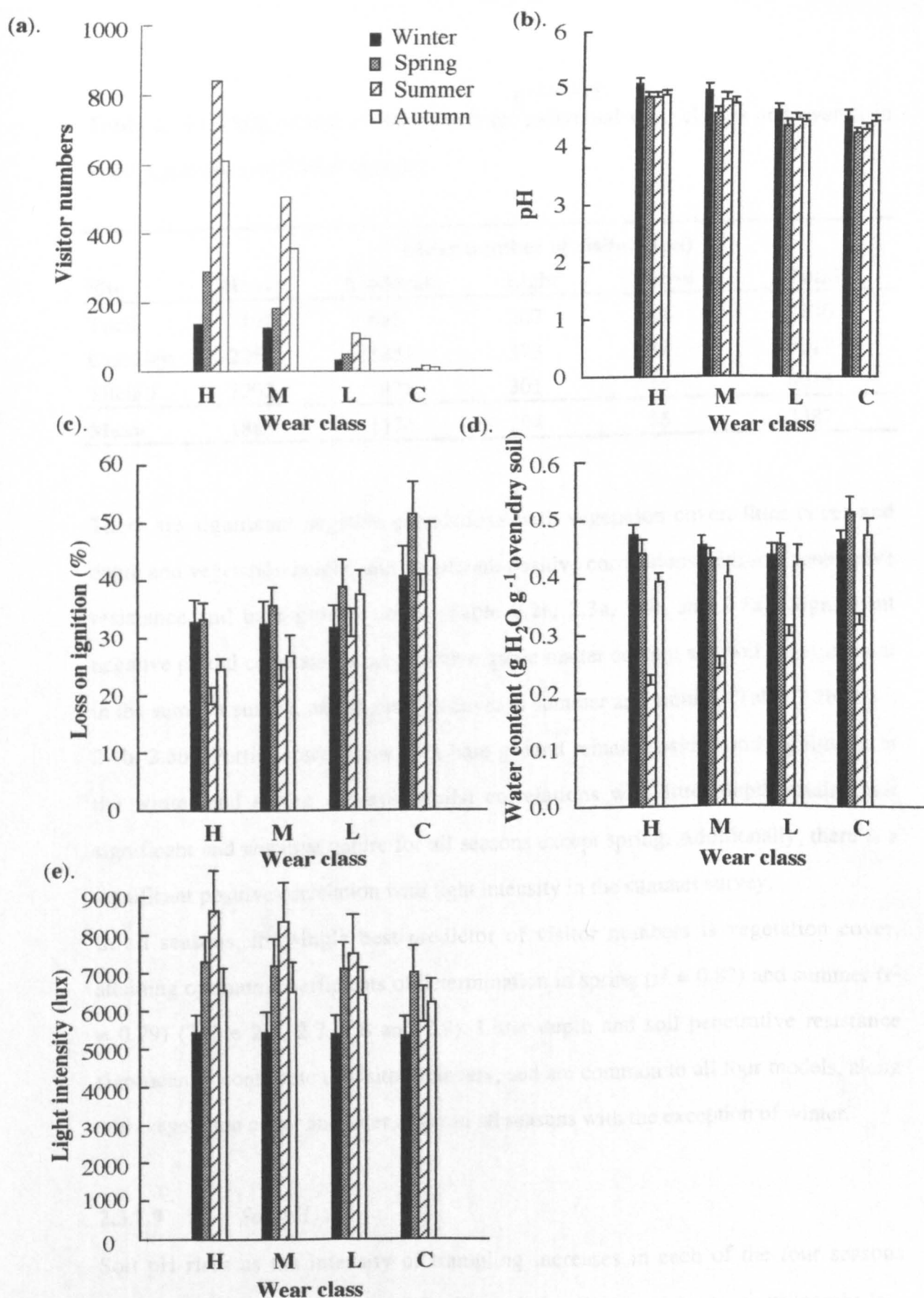


Fig. 2.4 - Total visitor numbers (a), soil pH (b), soil organic matter content (loss on ignition (c), soil water content (d) and light intensity (e) as a quadrat mean for all sites in the four wear classes in winter, spring, summer and autumn (H, heavily trampled; M, moderately trampled; L, lightly trampled; C, control).

Table 2.10 - Mean annual visitor counts for ^{per transect} individual wear classes and overall in Tocil, Crackley and Tilehill Woods.

Site	Mean number of visitors (pa)				Total
	Heavy	Moderate	Light	Control	
Tocil	1192	695	207	36	2130
Crackley	2256	1351	373	37	4017
Tilehill	2202	1476	301	36	4015
Mean	1883	1174	294	36	3387

There are significant negative correlations with vegetation cover, litter cover and depth and vegetation height, and significant positive correlations with soil penetrative resistance and bare ground cover (Table 2.2a, 2.3a, 2.4a and 2.5a). Significant negative partial correlations occur with organic matter content and soil water content in the summer survey, and vegetation cover in summer and autumn (Table 2.2b, 2.3b, 2.4b, 2.5b). Partial correlations with bare ground remain positive and significant in the winter and spring surveys, whilst correlations with litter depth retain their significant and negative nature for all seasons except spring. Additionally, there is a significant positive correlation with light intensity in the summer survey.

In all seasons, the single best predictor of visitor numbers is vegetation cover, attaining optimum coefficients of determination in spring ($r^2 = 0.82$) and summer ($r^2 = 0.79$) (Table 2.6, 2.7, 2.8 and 2.9). Litter depth and soil penetrative resistance significantly contribute to visitor numbers, and are common to all four models, along with vegetation cover and litter cover in all seasons with the exception of winter.

2.3.1.9 *Soil pH*

Soil pH rises as the intensity of trampling increases in each of the four seasons (Appendices 2.2, 2.3, 2.4 and 2.5). Trampled soils appear to be significantly less acidic than untrampled soils, but differences between wear classes in sites are not

always significant. Soil pH during winter is generally higher in all four wear classes than in the other three seasons (Fig. 2.4b).

Correlations with organic matter content and soil water content are negative and significant (Table 2.2a, 2.3a, 2.4a and 2.5a). There are positive significant correlations with bare ground cover, soil penetrative resistance and visitor numbers in all seasons. Partial correlations with organic matter and soil water content retain the negative significant relationship in autumn (Table 2.2b, 2.3b, 2.4b and 2.5b).

The best single predictor of soil pH is organic matter content in winter and autumn, litter cover in spring and soil water in summer, although the coefficients of determination are low in all cases (particularly in spring, where $r^2 = 0.13$) (Table 2.6, 2.7, 2.8 and 2.9). No single variable is common to all four models.

2.3.1.10 *Soil organic matter content*

The organic matter content of soil differs significantly between wear classes in summer and autumn, with soil organic matter content declining as trampling intensity increases. However, differences are not always significant, with no site differences between wear classes in winter and spring at all (Appendices 2.2, 2.3, 2.4 and 2.5). Organic matter reaches a maximum across the range of wear classes in spring, before falling to a minimum in summer (Fig. 2.4c).

The negative significant correlations with soil pH, penetrative resistance, visitor numbers and bare ground cover are most conspicuous during summer (Table 2.2a, 2.3a, 2.4a and 2.5a), and the positive significant partial correlation with soil water content illustrates a close association (Table 2.2b, 2.3b, 2.4b, 2.5b).

The best single predictor of soil organic matter content across the range of seasons is soil water content, particularly in winter ($r^2 = 0.76$) and autumn ($r^2 = 0.90$) (Table 2.6, 2.7, 2.8 and 2.9). Light intensity and soil water content are both variables that make significant contributions to all four seasonal models, as does bare ground cover and soil pH in all seasons with the exception of the summer survey.

2.3.1.11 *Soil water content*

Undisturbed surface soils are generally wetter than trampled soils, but differences are not always significant (Appendices 2.2, 2.3, 2.4 and 2.5). Indeed, undisturbed soils are marginally wetter than trampled soils in spring, summer and autumn. However, at times of peak precipitation in winter, the water content of trampled and undisturbed soils are very similar. Soils are up to twofolds drier in all wear class zones in summer compared to the other three seasons (Fig. 2.4d).

There are highly significant positive correlations with organic matter content, and significant negative correlations with soil pH, bare ground and soil penetrative resistance (Table 2.2a, 2.3a, 2.4a and 2.5a). The highest number of significant correlations occurs during summer, where there is a notable significant positive correlation with vegetation cover (Table 2.2b, 2.3b, 2.4b and 2.5b).

The best single predictor of soil water content is soil organic matter content (Table 2.6, 2.7, 2.8 and 2.9), and across all four seasonal models, soil organic matter significantly contribute to soil water content, as does soil penetrative resistance in all seasons with the exception of the summer survey.

2.3.1.12 *Light intensity*

Light intensity is significantly stronger at ground level along exposed trails than beneath undisturbed areas in the summer survey (Appendices 2.2, 2.3, 2.4 and 2.5). In trampled areas, maximum values are recorded in summer, followed by spring, autumn and finally winter (Fig. 2.4e). In the summer survey, light intensity of undisturbed areas is approximately two thirds of the strength evident in trail centres.

There are no general correlative trends between light intensity and the other environmental variables that are recurrent across all four seasons (Table 2.2a, 2.3a, 2.4a and 2.5a). However, during summer there are significant positive correlations with bare ground cover, soil penetrative resistance and visitor numbers, and significant negative correlations with litter cover, litter depth, vegetation cover and

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Fig. 2.11 - Summary of data presented in Appendices 2.6, 2.7, 2.8 and 2.9 of test parameters combined for all three sites for winter, spring, summer and autumn.

	Heavily trampled	Moderately trampled	Lightly trampled	Control untrampled
Number of species				
winter	6	29	50	36
spring	18	43	63	61
summer	13	45	81	71
autumn	11	37	57	48
Number of monocotyled- onous vascular plants				
winter	3	7	16	7
spring	4	9	12	9
summer	4	11	14	9
autumn	3	6	9	6
Number of dicotyledonous vascular plants				
winter	1	16	21	17
spring	12	22	38	40
summer	6	25	50	45
autumn	5	21	35	29
Number of mosses				
winter	2	6	10	9
spring	2	9	11	9
summer	3	8	13	13
autumn	3	9	10	10
Number of ferns				
winter	0	0	3	3
spring	0	0	2	3
summer	0	1	4	4
autumn	0	1	3	3
Mean Shannon's diversity index				
spring	0.12	0.29	0.47	0.42
summer	0.14	0.29	0.46	0.41
Species of ≥ 10 % frequency				
winter	<i>Poa</i> spp. ^a	<i>Poa</i> spp., <i>Eurynchium</i> <i>praelongum</i> , <i>Holcus</i> spp. ^b , <i>Hedera helix</i>	<i>Eurynchium</i> <i>praelongum</i> , <i>Deschampsia</i> <i>cespitosa</i> , <i>Holcus</i> spp., <i>Hedera helix</i> , <i>Rubus fruticosus</i> agg.	<i>Deschampsia</i> <i>cespitosa</i> , <i>Holcus</i> agg., <i>Hedera helix</i> , <i>Rubus fruticosus</i> , <i>Lonicera</i> <i>periclymenum</i> , <i>Ilex</i> <i>aquifolium</i> ^c

	Heavily trampled	Moderately trampled	Lightly trampled	Control untrampled
spring	<i>Poa</i> spp., <i>Eurynchium praelongum</i> , <i>Hyacinthoides non-scripta</i>	<i>Poa</i> spp., <i>Eurynchium praelongum</i> , <i>Hyacinthoides non-scripta</i> , <i>Anemone nemorosa</i> , <i>Holcus</i> spp., <i>Plantago major</i> , <i>Deschampsia cespitosa</i> , <i>Hedera helix</i>	<i>Hyacinthoides non-scripta</i> , <i>Anemone nemorosa</i> , <i>Holcus</i> spp., <i>Deschampsia cespitosa</i> , <i>Hedera helix</i> , <i>Galium aparine</i> , <i>Geum urbanum</i> , <i>Rubus fruticosus</i> agg., <i>Oxalis acetosella</i> , <i>Lonicera periclymenum</i>	<i>Hyacinthoides non-scripta</i> , <i>Anemone nemorosa</i> , <i>Ranunculus ficaria</i> , <i>Hedera helix</i> , <i>Galium aparine</i> , <i>Rubus fruticosus</i> agg., <i>Mercurialis perennis</i> , <i>Lonicera periclymenum</i>
summer	<i>Poa</i> spp.	<i>Poa</i> spp., <i>Eurynchium praelongum</i> , <i>Deschampsia cespitosa</i> , <i>Plantago major</i> , <i>Holcus</i> spp., <i>Lolium perenne</i> , <i>Rubus fruticosus</i> agg., <i>Hedera helix</i>	<i>Deschampsia cespitosa</i> , <i>Holcus</i> spp., <i>Rubus fruticosus</i> agg., <i>Hedera helix</i> , <i>Pteridium aquilinum</i> , <i>Dactylis glomerata</i> , <i>Lonicera periclymenum</i>	<i>Deschampsia cespitosa</i> , <i>Rubus fruticosus</i> agg., <i>Hedera helix</i> , <i>Pteridium aquilinum</i> , <i>Bromus ramosus</i> , <i>Urtica dioica</i> , <i>Lonicera periclymenum</i>
autumn	<i>Poa</i> spp.	<i>Poa</i> spp., <i>Rubus fruticosus</i> agg., <i>Deschampsia cespitosa</i> , <i>Hedera helix</i>	<i>Rubus fruticosus</i> agg., <i>Deschampsia cespitosa</i> , <i>Hedera helix</i> , <i>Holcus</i> spp., <i>Illex aquifolium</i>	<i>Rubus fruticosus</i> agg., <i>Hedera helix</i> , <i>Lonicera periclymenum</i> , <i>Pteridium aquilinum</i>
Most sensitive parameter^d	Winter	Spring	Summer	Autumn
	Vegetation height (7)	Vegetation height (15)	Vegetation height (14)	Vegetation height (6)

^a - mix of *Poa annua* and *P. pratensis*

^b - mix of *Holcus lanatus* and *H. mollis*

^c - sapling / seedling

^d - based on the highest number of significant differences (given in parentheses) between wear classes for individual species height, cover, leaf length and leaf width.

The highest diversity indices are recorded in the lightly trampled wear class in spring ($H = 0.47$) and summer ($H = 0.46$), before falling to a minimum in the heavily trampled wear class in spring ($H = 0.12$) and summer ($H = 0.14$). Species diversity across the range of wear classes are highest in Tocil Wood.

There are significant positive correlations with vegetation cover and height, leaf litter depth and leaf litter cover (summer only). Significant negative correlations are recorded with visitor numbers, soil penetrative resistance, bare ground cover and light intensity. The significant negative correlations with visitor numbers in spring ($r_s = -0.59$) and summer ($r_s = -0.54$) confirm that increasing levels of trampling result in a loss of species diversity.

2.3.2.1.3 Species frequency

Only *Deschampsia cespitosa* occurs across the range of wear classes in all four seasons, with *Eurynchium praelongum* and *Rubus fruticosus* agg. present in the four wear classes in spring, summer and autumn, and *Holcus* spp. in both spring and summer. The most abundant species in all seasons are *Rubus fruticosus* agg., *Hedera helix*, *Poa* spp., *Holcus* spp. and *Deschampsia cespitosa*, along with *Hyacinthoides non-scripta* and *Anemone nemorosa* in spring and *Pteridium aquilinum* in summer. Fourteen species are common to all four wear classes in the springtime survey, and the majority of these species are most frequent in the lightly trampled wear class zone. *Poa* spp., *Eurynchium praelongum*, *Plantago major*, *Stellaria media* and *Lolium perenne* are more frequent in the moderately trampled wear class than in the other wear class zones. Some species such as *Holcus* spp., *Oxalis acetosella* and *Geum urbanum* are mainly found along the edges of trails, whilst others, such as *Rubus fruticosus* agg., *Lonicera periclymenum*, *Pteridium aquilinum* and *Mercurialis perennis*, prefer undisturbed areas.

2.3.2.2 Cover

In the vast majority of cases, individual species cover increases as trampling intensity decreases (Appendices 2.6, 2.7, 2.8 and 2.9). Cover is significantly higher in untrampled areas for common species such as *Poa* spp. and *Rubus fruticosus* agg. in all four seasons, *Deschampsia cespitosa*, *Holcus* spp. and *Hedera helix* in winter and spring, *Hyacinthoides non-scripta*, *Anemone nemorosa* and *Stellaria holostea* in spring and *Digitalis purpurea* and *Silene dioica* in summer.

Poa spp., *Eurynchium praelongum*, *Taraxacum officinale*†, *Plantago major*, *Ranunculus* spp. and *Dicranum* spp. are the most abundant species in the moderate or heavy trampled zones. Thus, they are typical representatives of a sub-community tolerant of continual recreational trampling. Indeed, during the main growing seasons of spring and summer, correlations between visitor numbers and individual species

cover are negative and often significant for the majority of species present. The only species that exhibits a positive (but non-significant) relationship with visitor numbers is *Poa spp.* in both spring ($r_s = 0.26$; partial $r = 0.23$) and summer ($r_s = 0.22$; partial $r = 0.30$).

Away from the trail edge, vegetation in undisturbed areas is dominated by upright herbaceous species such as *Rubus fruticosus agg.* (with a mean summer cover of 33 %), *Pteridium aquilinum* (with a mean summer cover of 39 %), *Hyacinthoides non-scripta* (with a mean spring cover of 54 %), *Ilex aquifolium* (sapling) and three *Dryopteris spp.*

2.3.2.3 Height

Vegetation height increases dramatically as trampling intensity decreases, but there is a great deal of variability in response amongst species (particularly in the untrampled control wear class) (Appendices 2.6, 2.7, 2.8 and 2.9). Plants are significantly shorter in trampled areas for *Poa spp.*, *Deschampsia cespitosa*, *Holcus spp.*, *Hedera helix* and *Rubus fruticosus agg.* in all four seasons, for *Galium aparine* in winter and spring, for *Mercurialis perennis*, *Plantago major* and *Geum urbanum* in spring and summer and for *Silene dioica* in winter and summer.

The tallest species found growing in undisturbed vegetation during summer is *Heracleum sphondylium* at 170 cm, and the tallest in the winter survey is *Rubus fruticosus agg.*, which measures 25 cm. This contrasts with the tallest species recorded in trail centres during summer (*Holcus spp.* at 7 cm) and in winter (*Poa spp.* at just 1.4 cm).

2.3.2.4 Leaf length

Increasing levels of trampling result in the reduction in leaf lengths of most vascular plant species (Appendices 2.6, 2.7, 2.8, 2.9). The leaves of untrampled plants are significantly longer for *Poa spp.*, *Hedera helix*, *Deschampsia cespitosa* and *Rubus*

fruticosus in all four seasons, for *Holcus spp.* in winter, spring and summer, for *Lolium perenne* in winter and autumn, and for *Geum urbanum* in spring and summer. With leaves measuring 60 cm in length, *Juncus spp.* has the longest leaves of any undisturbed species in summer, contrasting with the longest leaves in the heavily trampled zone recorded for *Taraxacum officinale* at 13 cm. This compares with winter survey leaf lengths of undisturbed and heavily trampled plants of *Deschampsia cespitosa* at 22 cm and 4 cm long respectively.

2.3.2.5 *Leaf width*

Paralleling the reduction in leaf length, there is also an obvious reduction in leaf width in response to the increasing levels of wear (Appendices 2.6, 2.7, 2.8 and 2.9). Leaves are significantly wider in undisturbed zones for *Hedera helix* and *Rubus fruticosus* agg. in all four seasons, for *Deschampsia cespitosa* in spring, summer and autumn, and for *Poa spp.*, *Geum urbanum* and *Brachypodium sylvaticum* in spring and summer.

In the summer survey, untrampled plants of *Arctium minus* have the widest leaves at 18 cm, and in the heavily trampled zone the widest leaves belong to *Plantago major* at 1.6 cm. In the winter survey, *Digitalis purpurea* possesses the widest leaves at 9 cm, comparing with 1 cm wide leaves *Geum urbanum* in the heavily trampled zone.

2.3.3 *Ordination analyses*

The CA and DCA ordinations induce eigenvalues for the first four axes from the spring and summer data sets (Table 2.12). In both seasons, the first ordination axis possesses the highest eigenvalue and accounts for the highest proportion in species variation (spring survey: n = 326 quadrats; summer survey: n = 325 quadrats). Thus axis one captures a substantial amount of the variation in vegetation cover. The second axis provides the second highest range of eigenvalues and species variance, with third and fourth axes eigenvalues becoming progressively smaller. On the

assumption that the first two axes display the ecologically relevant information, subsequent analyses are concentrated on these two axes only.

Table 2.12 - Eigenvalues and the variance of species data produced by correspondence analysis (CA) and detrended correspondence analysis (DCA) for the first four axes in the spring and summer data sets.

Season		Axis			
		1	2	3	4
Spring					
CA	Eigenvalue	0.683	0.430	0.419	0.358
	Variance ^a	14.3 (14.3)	8.9 (23.3)	8.7 (32.0)	7.5 (39.5)
DCA	Eigenvalue	0.683	0.414	0.360	0.228
	Variance	14.3 (14.3)	8.6 (22.9)	7.5 (30.4)	4.8 (35.2)
Summer					
CA	Eigenvalue	0.661	0.427	0.411	0.364
	Variance	13.0 (13.0)	8.4 (21.4)	8.1 (29.5)	7.2 (36.7)
DCA	Eigenvalue	0.661	0.400	0.329	0.277
	Variance	13.0 (13.0)	7.9 (20.9)	6.5 (27.4)	5.5 (32.8)

^a - percentage variance of species data with cumulative percentage variances shown in parentheses

The DCA analysis arranges sites and species along the first two axes which are interpreted in separate ordination plots for both spring (Fig. 2.5a & 2.5b) and summer surveys (Fig. 2.6a & 2.6b). Common to both surveys, *Poa spp.* and *Plantago major* both score highly on the first axis, whereas *Hedera helix*, *Rubus fruticosus agg.* and *Lonicera periclymenum* have low scores. *Anemone nemorosa* and *Hyacinthoides non-scripta* in the spring survey and *Pteridium aquilinum* in the summer survey also have low scores. This suggests that the first axis may represent a measure of trampling tolerance. *Lonicera periclymenum* scores highly on axis two in both seasons, and *Anemone nemorosa* and *Ranunculus ficaria* have low scores in spring. Both *Deschampsia cespitosa* and *Holcus spp.* have low scores low in summer but not in spring.

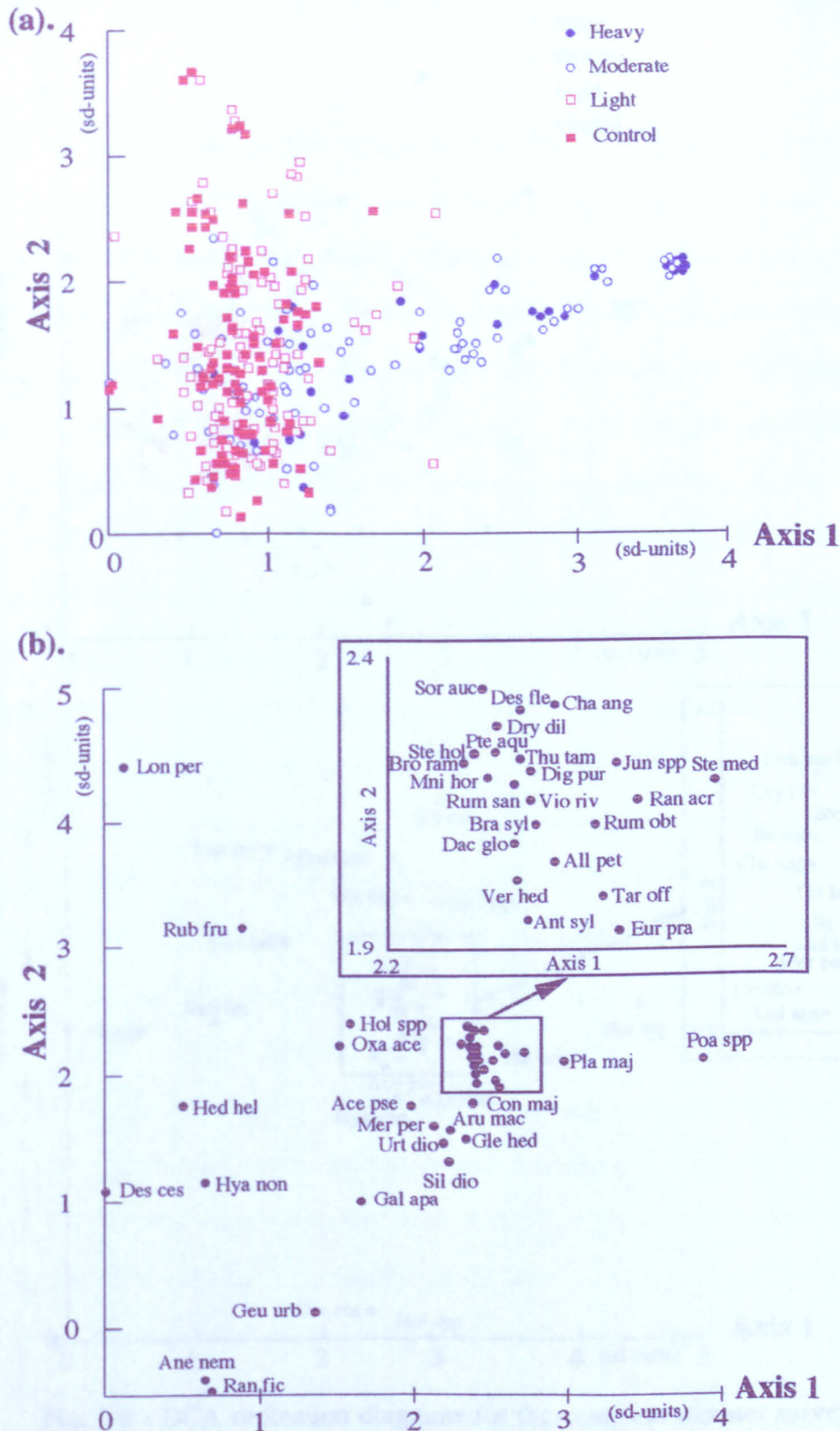


Fig. 2.5 - DCA ordination diagrams for the complete spring survey data set ($n = 326$ quadrats), presented as (a). quadrats plotted by their scores on the first two axes from the DCA analysis, and (b). 43 of the commonest species plotted by their scores on the first two axes from the DCA analysis, with rare species downweighted. (Eur pra = *Eurynchium praelongum*; Rub fru = *Rubus fruticosus*; Hed hel = *Hedera helix*; Gle hed = *Glechoma hederacea*; Sil dio = *Silene dioica*; Stel hol = *Stellaria holostea*; Poa spp = *Poa annua* / *P. pratensis* mix; Oxa ace = *Oxalis acetosella*; Mer per = *Mercurialis perennis*; Gal apa = *Galium aparine*; Hya non = *Hyacinthoides non-scripta*; Urt dio = *Urtica dioica*; Pla maj = *Plantago major*; Ver hed = *Veronica hederifolia*; Geu urb = *Geum urbanum*; Des ces = *Deschampsia cespitosa*; Bra syl = *Brachypodium sylvaticum*; Hol spp = *Holcus lanatus* / *H. mollis* mix; Pte aqu = *Pteridium aquilinum*; Ace pse = *Acer pseudoplatanus* (seedling); Mni hor = *Mnium hornum*; Ste med = *Stellaria media*; Dac glo = *Dactylis glomerata*; Rum obt = *Rumex obtusifolius*; Cha ang = *Chamaenerion angustifolium*; Ran acr = *Ranunculus acris*; Lon per = *Lonicera periclymenum*; Bro ram = *Bromus ramosus*; Dry dil = *Dryopteris dilatata*; Jun spp = *Juncus* spp; Des fle = *Deschampsia flexuosa*; Dig pur = *Digitalis purpurea*; Thu tam = *Thuidium tamariscinum*; Ane nem = *Anemone nemorosa*; Ran fic = *Ranunculus ficaria*; Tar off = *Taraxacum officinale*; Ant syl = *Anthriscus sylvestris*; Rum san = *Rumex sanguineus*; Con maj = *Conopodium majus*; All pet = *Alliaria petiolata*; Sor auc = *Sorbus aucuparia*; Des fle = *Deschampsia flexuosa*; Vio riv = *Viola riviniana*).

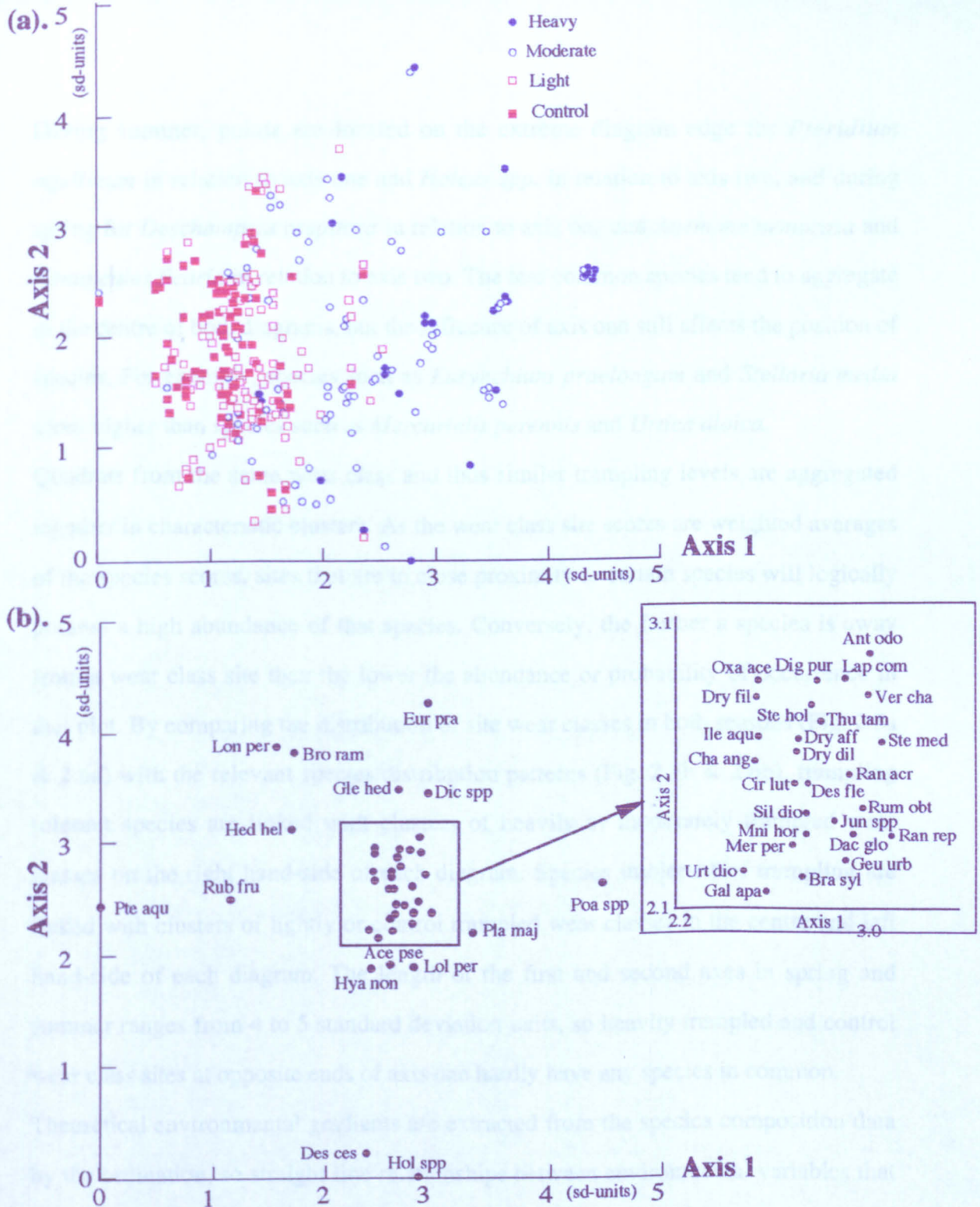


Fig. 2.6 - DCA ordination diagrams for the complete summer survey data set ($n = 325$ quadrats), presented as (a). quadrats plotted by their scores on the first two axes from the DCA analysis, and (b). 42 of the commonest species plotted by their scores on the first two axes from the DCA analysis, with rare species downweighted (Eur pra = *Eurynchium praelongum*; Rub fru = *Rubus fruticosus*; Hed hel = *Hedera helix*; Gle hed = *Glechoma hederacea*; Sil dio = *Silene dioica*; Stel hol = *Stellaria holostea*; Poa spp = *Poa annua* / *P. pratensis* mix; Oxa ace = *Oxalis acetosella*; Mer per = *Mercurialis perennis*; Gal apa = *Galium aparine*; Hya non = *Hyacinthoides non-scripta*; Urt dio = *Urtica dioica*; Dry fil = *Dryopteris filix-mas*; Pla maj = *Plantago major*; Ver cha = *Veronica chamaedrys*; Geu urb = *Geum urbanum*; Lap com = *Lapsana communis*; Des ces = *Deschampsia cespitosa*; Bra syl = *Brachypodium sylvaticum*; Hol spp = *Holcus lanatus* / *H. mollis* mix; Pte aqu = *Pteridium aquilinum*; Ace pse = *Acer pseudoplatanus* (seedling); Mni hor = *Mnium hornum*; Ste med = *Stellaria media*; Ran rep = *Ranunculus repens*; Dac glo = *Dactylis glomerata*; Rum obt = *Rumex obtusifolius*; Ile aqu = *Ilex aquifolium* (sapling); Cha ang = *Chamaenerion angustifolium*; Cir lut = *Circaea lutetiana*; Ran acr = *Ranunculus acris*; Dic spp = *Dicranum spp*; Lon per = *Lonicera perichlymenum*; Bro ram = *Bromus ramosus*; Dry dil = *Dryopteris dilatata*; Lol per = *Lolium perenne*; Jun spp = *Juncus spp*; Des fle = *Deschampsia flexuosa*; Ant odo = *Anthoxanthum odoratum*; Dig pur = *Digitalis purpurea*; Dry aff = *Dryopteris affinis*; Thu tam = *Thuidium tamariscinum*).

During summer, points are located on the extreme diagram edge for *Pteridium aquilinum* in relation to axis one and *Holcus spp.* in relation to axis two, and during spring for *Deschampsia cespitosa* in relation to axis one and *Anemone nemorosa* and *Ranunculus ficaria* in relation to axis two. The less common species tend to aggregate in the centre of both diagrams, but the influence of axis one still affects the position of species. For example, species such as *Eurynchium praelongum* and *Stellaria media* score higher than species such as *Mercurialis perennis* and *Urtica dioica*.

Quadrats from the same wear class and thus similar trampling levels are aggregated together in characteristic clusters. As the wear class site scores are weighted averages of the species scores, sites that are in close proximity to certain species will logically possess a high abundance of that species. Conversely, the further a species is away from a wear class site then the lower the abundance or probability of occurrence in that plot. By comparing the distribution of site wear classes in both seasons (Fig. 2.5a & 2.6a) with the relevant species distribution patterns (Fig. 2.5b & 2.6b), trampling tolerant species are linked with clusters of heavily or moderately trampled wear classes on the right hand-side of each diagram. Species intolerant of trampling are linked with clusters of lightly or control trampled wear classes in the centre and left hand-side of each diagram. The length of the first and second axes in spring and summer ranges from 4 to 5 standard deviation units, so heavily trampled and control wear class sites at opposite ends of axis one hardly have any species in common.

Theoretical environmental gradients are extracted from the species composition data by the ordination, so straight line relationships between environmental variables that influence species and the ordination axes are expected. DCA scores for axis one yield significant negative ranked correlations with vegetation cover and height and litter cover and depth in both seasonal surveys, and with soil organic matter and water content in the summer survey only (Table 2.13). Significant positive correlations are found with visitor numbers, bare ground cover and soil penetrative resistance in both seasons, and with soil pH and light intensity in summer.

The relationships with axis two are more complex, with significant negative correlations with vegetation cover and litter depth in both seasons, and with vegetation height in summer and soil pH in spring (Table 2.13). There are also low, significant positive correlations with soil penetrative resistance, visitor numbers, soil organic matter, soil water content and light intensity in spring. Therefore, the second axis during spring seems to be more influenced by trampling intensity than in summer.

Table 2.13 - Spearman rank intraset correlation coefficients ($100 \times r_s$) of environmental variables with the first two DCA axes for the spring and summer data sets.

Variable	Spring		Summer	
	Axis 1	Axis 2	Axis 1	Axis 2
1 Vegetation cover	-70***	-28**	-76***	-26**
2 Bare ground cover	60***	10	76***	15
3 Leaf litter cover	-38***	20	-69***	-7
4 Leaf litter depth	-67***	-26**	-76***	-23*
5 Soil penetrative resistance	70***	24*	83***	15
6 Vegetation height	-71***	-6	-81***	-21*
7 Visitor numbers	74***	23*	80***	9
8 Soil pH	12	-37***	41***	-11
9 Soil organic matter	-9	32**	-49***	6
10 Soil water content	-15	21*	-34***	9
11 Light intensity	19	25*	30**	-9

*** sig. at $p \leq 0.001$; ** sig. at $p \leq 0.01$; * sig. at $p \leq 0.05$; $n = 100$

The multiple regression analysis on the first two DCA axes illustrates whether the environmental variables are sufficient to significantly predict the variation in species composition represented by the axes. In both spring and summer, visitor numbers contributes significantly to the explanation of the first axis, whereas the other environmental variables do not (Table 2.14). Multiple regression analysis reveals that vegetation cover and height in spring, and litter depth in summer significantly

contribute to the explanation of the second axis. However, overall relationships with environmental variables are complex, with huge variation between sites of the same wear class and amongst species.

Table 2.14 - Multiple regression of the first two DCA axes, indicating those environmental variables that significantly contributed to the explanation of axes for the spring and summer data sets.

Season	Axis	Significant predictors ^a	r ²	F
Spring	1	Visitor numbers (p = 0.048*)	0.66	14.0***
	2	Vegetation height (p = 0.004**); vegetation cover (p = 0.008**) 0.43	5.4***	
Summer	1	Visitor numbers (p = 0.0004***)	0.72	18.4***
	2	Litter depth (p = 0.019*); vegetation cover (p = 0.059)	0.22	2.0*

^a - **spring** (vegetation cover (arcsine transformed); vegetation height, visitor numbers (both square root transformed); **summer** (visitor numbers (square root transformed); leaf litter depth (log(10) transformed), vegetation cover (arcsine transformed); *** sig. at p ≤ 0.001; ** sig. at p ≤ 0.01; * sig. at p ≤ 0.05; n = 100

2.3.4 Plant strategies of species

2.3.4.1 Growth form classification

Individual species are classified into either rosette, tussock / tufted, prostrate, erect herbaceous or upright woody growth forms based on their morphological characteristics. The relative percent frequency of growth forms peculiar to each wear class are plotted for spring (Fig. 2.7a), summer (Fig. 2.7b), autumn (Fig. 2.8a).and winter surveys (Fig. 2.8b). Similar seasonal trends in the relative proportions of particular growth forms are apparent across the range of wear classes.

The relative proportions of rosette, tussock / tufted and prostrate species are higher in heavily and moderately trampled wear classes compared with lightly and control trampled wear classes, and increase with the intensity of wear. In contrast, the relative proportion of erect herbaceous and upright woody species declines with increasing intensity of trampling. These trends are particularly evident during the main growing seasons of spring and summer.

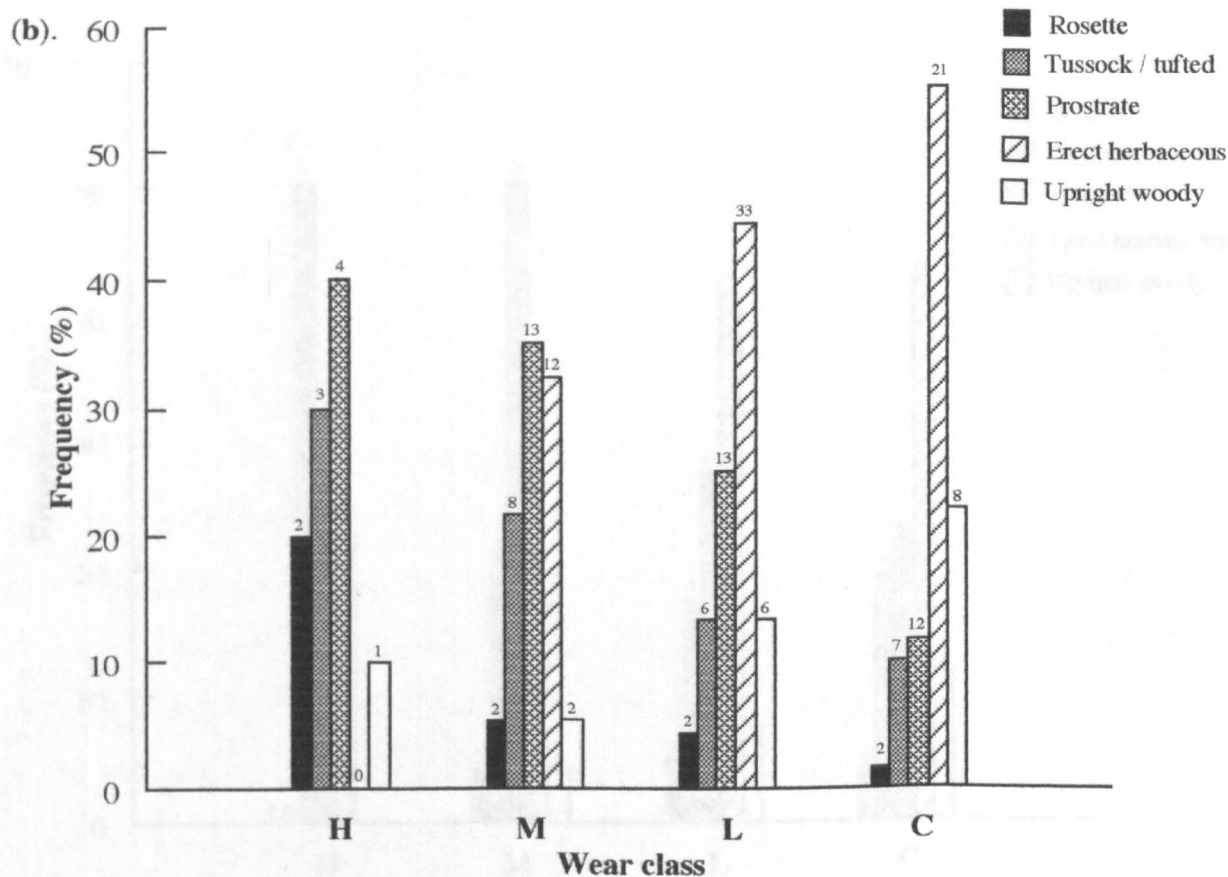
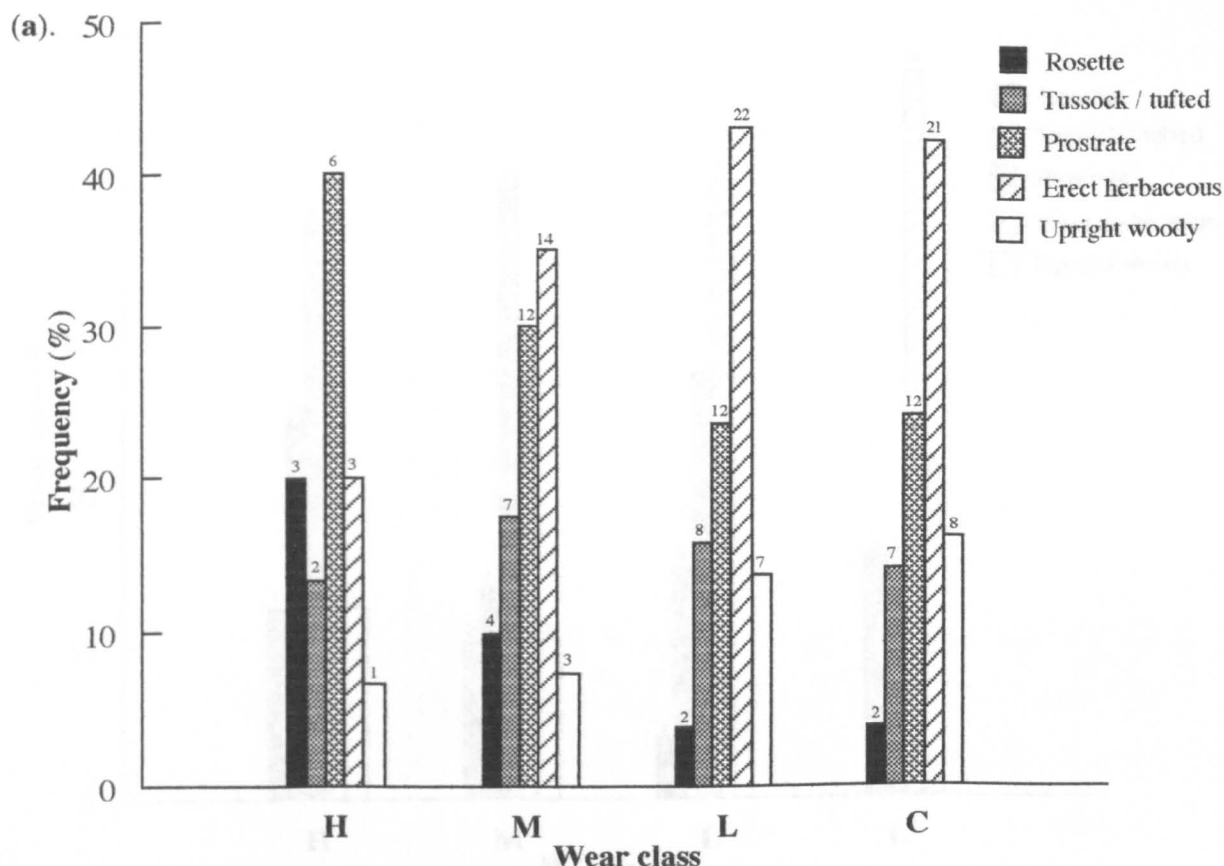


Fig. 2.7 - Frequency distribution (%) of growth-forms in the four wear classes combined for Tocil, Tilehill and Crackley Woods in (a) spring and (b) summer (H, heavily trampled; M, moderately trampled; L, lightly trampled; C, control). The numbers above the columns indicate the number of species in each category.

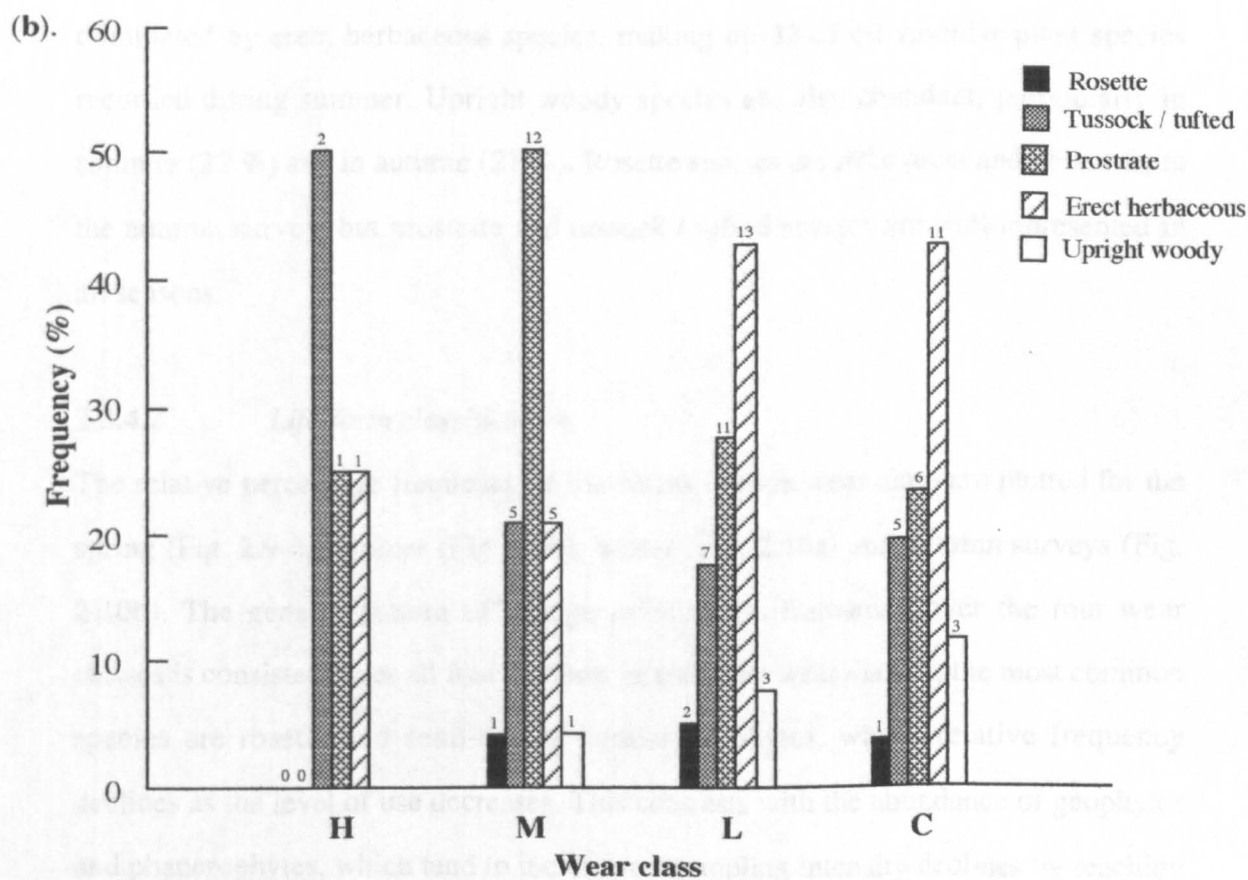
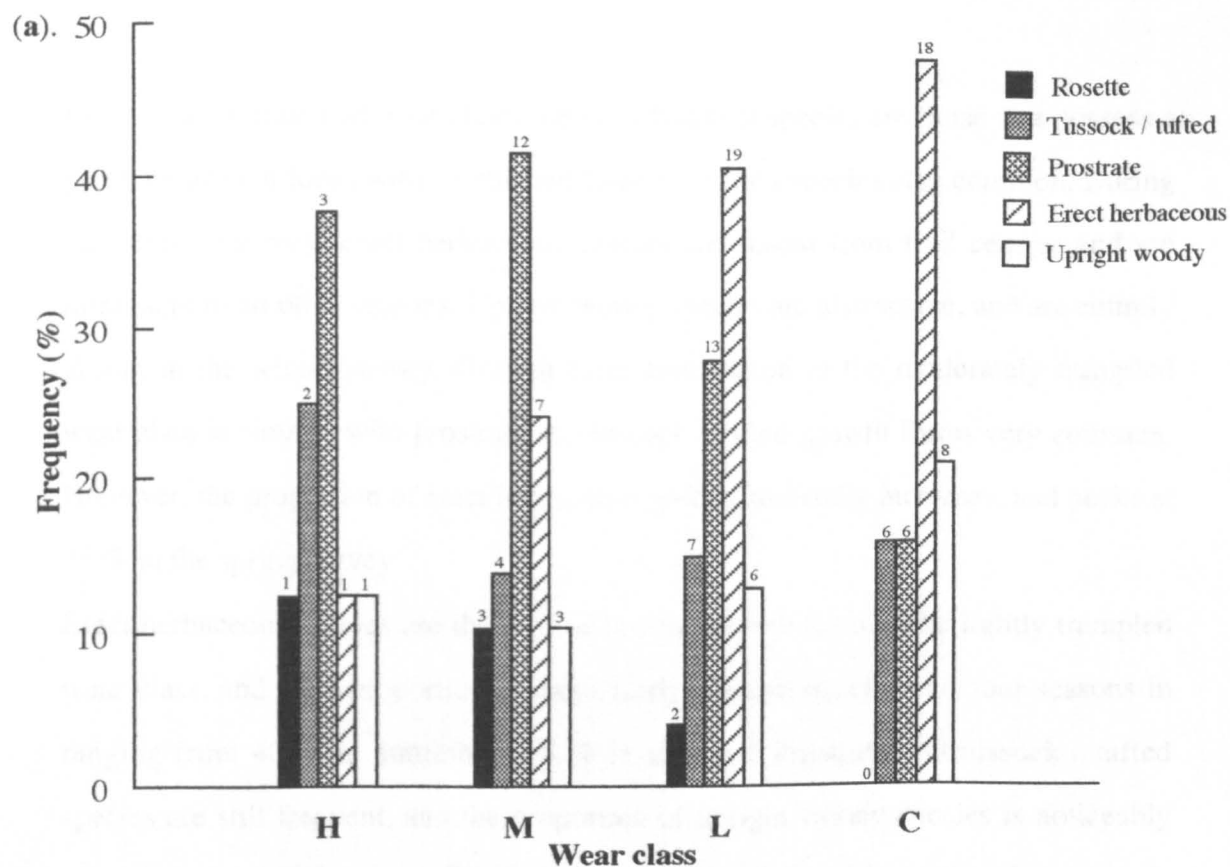


Fig. 2.8 - Frequency distribution (%) of growth-forms in the four wear classes combined for Tocil, Tilehill and Crackley Woods in (a) autumn and (b) winter (H, heavily trampled; M, moderately trampled; L, lightly trampled; C, control). The numbers above the columns indicate the number of species in each category.

In the heavily trampled wear class, the most frequent species are those that possess a prostrate growth form, with rosette and tussock / tufted species also common. During the summer survey, erect herbaceous species are absent from trail centres and are infrequent in all other seasons. Upright woody species are also scarce, and are entirely absent in the winter survey. Growth form distribution in the moderately trampled wear class is similar, with prostrate and tussock / tufted growth forms very common. However, the proportion of erect herbaceous species markedly increases, and peaks at 35 % in the spring survey.

Erect herbaceous species are the most abundant growth form in the lightly trampled wear class, and their proportion remains fairly consistent across all four seasons in ranging from 40 % in autumn to 44 % in summer. Prostrate and tussock / tufted species are still frequent, and the proportion of upright woody species is noticeably greater than in trail centres. Finally, the vegetation located in undisturbed areas is dominated by erect herbaceous species, making up 33 of 60 vascular plant species recorded during summer. Upright woody species are also abundant, particularly in summer (22 %) and in autumn (21 %). Rosette species are infrequent and absent from the autumn survey, but prostrate and tussock / tufted species are well represented in all seasons.

2.3.4.2 *Life-form classification*

The relative percentage frequency of life-forms in each wear class are plotted for the spring (Fig. 2.9a), summer (Fig. 2.9b), winter (Fig. 2.10a) and autumn surveys (Fig. 2.10b). The general pattern of change in life-form frequency over the four wear classes is consistent over all four seasons. In trampled wear classes, the most common species are rosette and semi-rosette hemicryptophytes, whose relative frequency declines as the level of use decreases. This contrasts with the abundance of geophytes and phanerophytes, which tend to increase as trampling intensity declines by reaching a maximum in the control wear class. Protohemicryptophytes, chamaephytes and

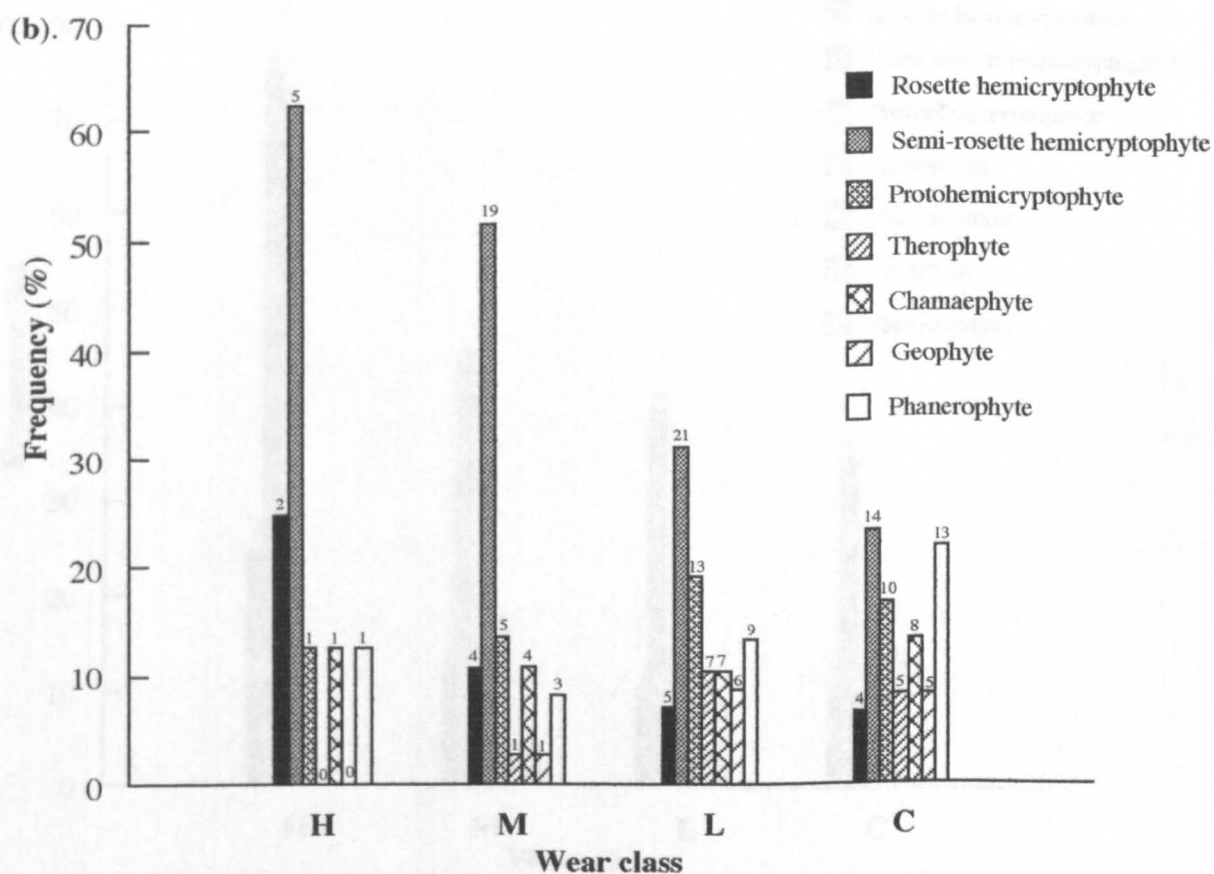
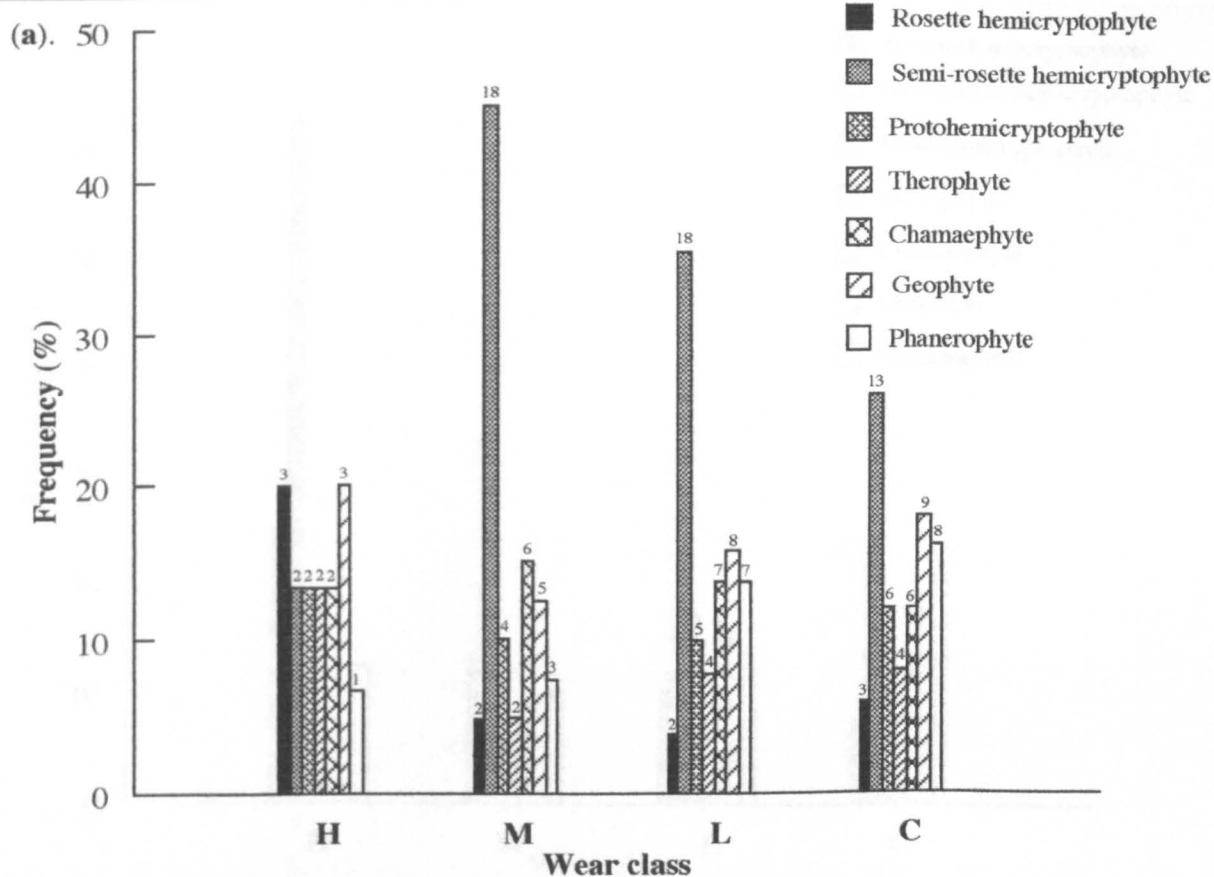


Fig. 2.9 - Frequency distribution (%) of life-forms in the four wear classes combined for Tocil, Tilehill and Crackley Woods in (a) spring and (b) summer (H, heavily trampled; M, moderately trampled; L, lightly trampled; C, control). The numbers above the columns indicate the number of species in each category.

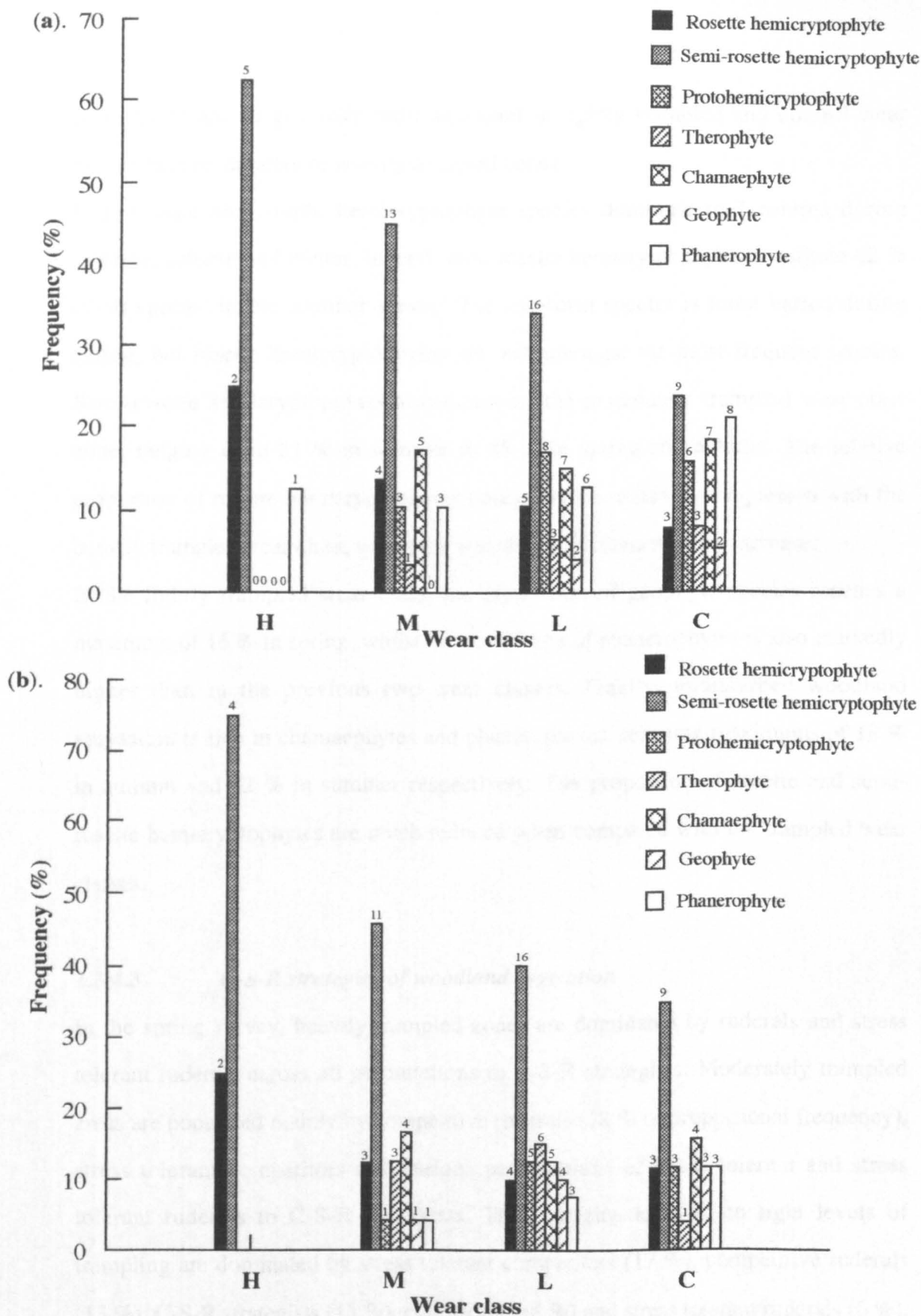


Fig. 2.10 - Frequency distribution (%) of life-forms in the four wear classes combined for Tocil, Tilehill and Crackley Woods in (a) autumn and (b) winter (H, heavily trampled; M, moderately trampled; L, lightly trampled; C, control). The numbers above the columns indicate the number of species in each category.

therophytes are all generally more abundant in lightly trampled and control wear classes than moderately or heavily trampled zones.

Semi-rosette and rosette hemicryptophyte species dominate trail centres during summer, autumn and winter. Indeed, semi-rosette hemicryptophytes constitute 62 % of all species in the summer survey. The life-form spectra is more varied during spring, but rosette hemicryptophytes are still amongst the most frequent species. Semi-rosette hemicryptophytes also dominate the moderately trampled wear class zone, ranging from 51 % in summer to 45 % in spring and autumn. The relative proportion of rosette hemicryptophytes noticeably decreases in comparison with the heavily trampled wear class, whilst the abundance of chamaephytes increase.

In the lightly trampled wear class, the proportion of geophyte species reaches a maximum of 16 % in spring, whilst the abundance of phanerophytes is also markedly higher than in the previous two wear classes. Finally, undisturbed woodland vegetation is rich in chamaephytes and phanerophytes, reaching maximums of 18 % in autumn and 22 % in summer respectively. The proportion of rosette and semi-rosette hemicryptophytes are much reduced when compared with the trampled wear classes.

2.3.4.3 *C-S-R strategies of woodland vegetation*

In the spring survey, heavily trampled zones are dominated by ruderals and stress tolerant ruderals across all permutations to C-S-R strategists. Moderately trampled areas are populated mainly by competitive ruderals (18 % of proportional frequency), stress tolerant competitors and various permutations of stress tolerant and stress tolerant ruderals to C-S-R strategists. Trail margins exposed to light levels of trampling are dominated by stress tolerant competitors (17 %), competitive ruderals (15 %), C-S-R strategists (13 %), competitors (8 %) and stress tolerant ruderals (6 %). Undisturbed woodland vegetation are dominated by stress tolerant competitors (16 %), competitive ruderals (12 %), C-S-R strategists (12 %) and competitors (10 %).

In the summer survey, heavily trampled plants are dominated by ruderals (27 %) and ruderals to C-S-R strategists (18 %). Zones receiving moderate levels of trampling are mainly populated by C-S-R strategists (24 %), competitive ruderals (11 %) and intermediates between the two (13 %). The frequency of ruderals declines to 8 %. Competitive ruderals (16 %), C-S-R strategists (17 %) and stress tolerant competitors (16 %) are the most abundant species in lightly trampled areas, with competitors (9 %) and stress tolerators (9 %) also abundant. The widest range of intermediate strategies are recorded in the undisturbed woodland zone, where stress tolerant competitors (22 %), competitive ruderals (15 %), C-S-R strategists (13 %), competitors (8 %) and stress tolerators (7 %) comprise the most abundant strategies.

Chapter 3

THE IMPACT OF EXPERIMENTAL TRAMPLING ON WOODLAND GROUND FLORA SUB-COMMUNITIES DOMINATED BY *Hyacinthoides non-scripta*, *Rubus fruticosus* agg. AND *Pteridium aquilinum*

3.1 Introduction

The impacts associated with recreational trampling in woodlands are ^{quantified} ~~classified~~ using an adaptation of the standardised experimental trampling protocol method devised by Cole & Bayfield (1993). The responses of several different woodland field layer sub-community types to trampling are ascertained by modelling the amount of trampling with the amount of impact. Information is synthesised on ecosystem damage (i.e.: the extent of change occurring as a direct result of trampling disturbance) and recovery (i.e.: the ability to revert back to pre-disturbance conditions once trampling ceases). The overall aim is ^{to} define the ecological carrying capacity of woodland stands for recreation. From a management perspective, this allows resource managers to manage use and access by knowing that stands are either sensitive to or tolerant of trampling.

3.1.1 Research objectives

- To quantify the nature of the relationship between vegetation or soil characteristics with experimental trampling in field layer stands dominated by *Rubus fruticosus* agg. and *Pteridium aquilinum* and *Hyacinthoides non-scripta*.
- To estimate the carrying capacity of the three common ground flora ^{Species} ~~types~~ for recreation by adapting the standardised protocol method denoted by Cole & Bayfield (1993). Response of vegetation and soils to trampling is considered in terms of durability indices of resistance (the ability of a vegetation type to resist change when trampled), resilience (the ability of a vegetation type to recover from trampling) and tolerance (the ability of a vegetation type to both resist and recover from trampling).
- To determine whether the principal influence on vegetation is the final sum of loads or the trampling periodicity.
- To examine the influence of shade on carrying capacity by sampling ground flora vegetation of partially shaded deciduous stands and heavily shaded coniferous stands.

- To recommend recreation management priorities for woodlands which help resource managers assess the likely impacts associated with recreational access.

3.2 Materials and Methods

3.2.1 Fieldwork sites

Homogeneous, undisturbed stands of *Rubus fruticosus* agg., *Pteridium aquilinum* and *Hyacinthoides non-scripta* were selected in Tocil Wood, Tilehill Wood and Brandon Wood (plantation dominated) (Table 3.1). All woodlands are W10 *Quercus robur* - *Pteridium aquilinum* - *Rubus fruticosus* woodland communities (Rodwell 1991).

Table 3.1 - Fieldwork sites for experimental trampling trials

Site	Field layer dominant	Canopy dominants	Light intensity ^a	Overstorey canopy cover ^b
Tocil Wood SP 303 764	<i>Hyacinthoides non-scripta</i> (deciduous - partial shade)	<i>Quercus robur</i> , <i>Acer pseudoplatanus</i> , <i>Fraxinus excelsior</i>	0.7	25
	<i>Pteridium aquilinum</i>		0.8	40
Brandon Wood^d SP 395 766	<i>Hyacinthoides non-scripta</i> (coniferous - closed shade)	<i>Pinus sylvestris</i> , <i>Betula pendula</i>	0.3	70
Tilehill Wood SP 280 790	<i>Rubus fruticosus</i> agg.	<i>Quercus robur</i> , <i>Acer pseudoplatanus</i> , <i>Pinus sylvestris</i>	0.6	35

^a - ratio of mean light intensity relative to full light intensity estimated before the experimental trials using a hand held light SensorMeter

^b - mean percent canopy cover at the time of trampling

Detailed site descriptions of Tocil and Tilehill Woods are given in section 2.2.1. Brandon Wood (SP 395 775) is a 65 ha freehold Forestry Commission plantation on the urban fringe of Coventry. The complex mosaic of *Pinus sylvestris* and *Larix decidua* stands are interspersed with mixed stands of *Betula pendula*, *Picea abies*, *Quercus robur*, *Betula pendula* and *Sorbus aucuparia*. Flora and fauna are generally impoverished as a consequence of lack of management, damage from forestry

practices and a poor woodland structure. Motorbike scrambling, dog walking and vandalism are recognised recreational impacts (Healy pers. commn. 1994).

3.2.2 Vegetation types

Detailed descriptions of the deciduous (Plate 3.1) and coniferous (Plate 3.2) *Hyacinthoides non-scripta* dominated sub-communities, the *Pteridium aquilinum* dominated sub-community (Plate 3.3) and the *Rubus fruticosus* agg. dominated sub-community (Plate 3.4) are given in Appendix 3.1.

3.2.3 Experimental methods and data collection

3.2.3.1 Treatment lane layout

Four replicate sets of experimental trampling lanes were set up in areas of homogeneous ground flora dominated by almost pure stands of either *Rubus fruticosus* agg., *Pteridium aquilinum* or *Hyacinthoides non-scripta* (deciduous and coniferous stands).

Sets of sampling lanes were randomly located within the pre-defined areas according to the random walk procedure delineated by Gilbertson *et al.* (1985). Treatments from zero to 500 passes were randomly assigned to each of the six lanes of each set. Trampling lanes measured 1.5 m long by 0.5 m wide, with a separating buffer strip of 0.4 m (Fig. 3.1). Lanes were wide enough to accommodate a 30 cm wide sampling quadrat, and dimensions were considered to be the minimum required to sample a representative stand of vegetation and be trampled in a normal manner (Cole & Bayfield 1993). The total area of vegetation required was approximately 30 m².

Plate 3.1 - *Hyacinthoides non-scripta* (deciduous woodland cover) dominated sub-community (Tocil Wood; SP 303 755, April 1995)



Plate 3.2 - *Hyacinthoides non-scripta* (coniferous woodland cover) dominated sub-community (Brandon Wood; SP 393 768, April 1995)



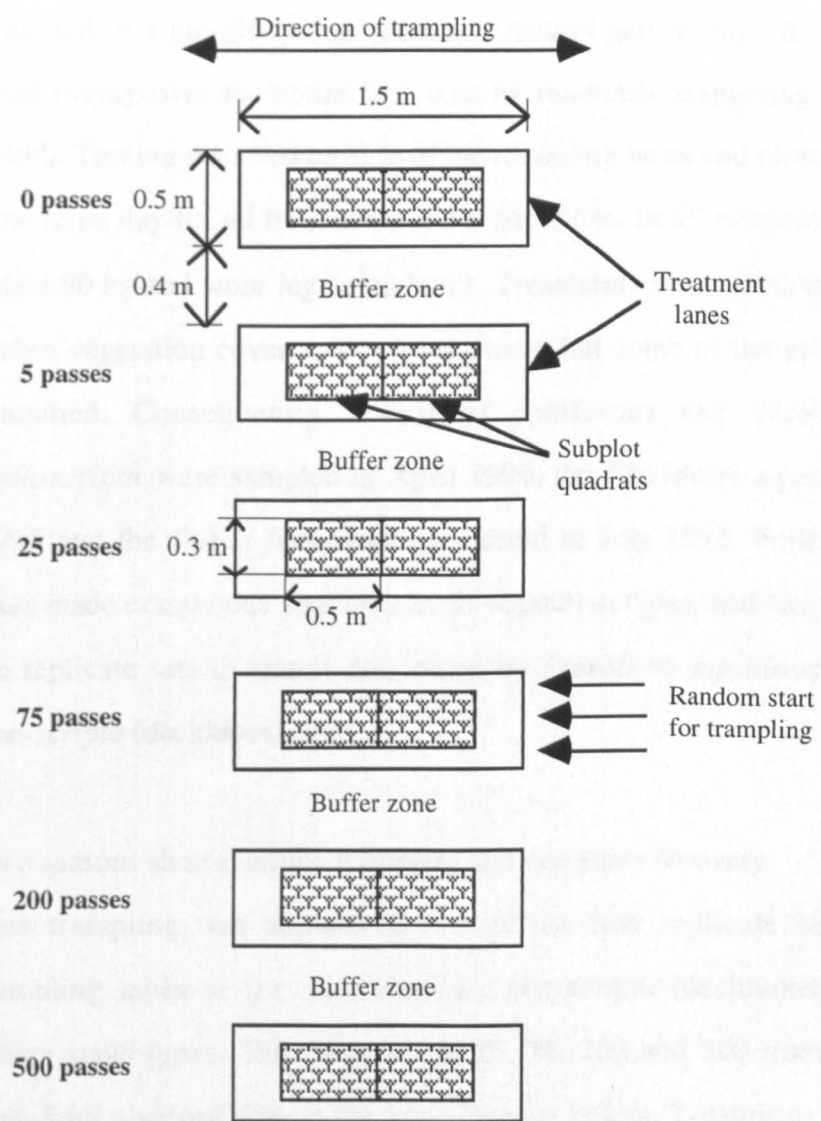
Plate 3.3 - *Pteridium aquilinum* dominated sub-community (Tocil Wood; SP 303 754, June 1996)



Plate 3.4 - *Rubus fruticosus* agg. dominated sub-community (Tilehill Wood; SP 279 789, July 1996)



Fig. 3.1 - The arrangement of each of the four replicate sets of experimental trampling lanes (0, 5, 25, 75, 200 and 500 passes) in stands dominated by *Pteridium aquilinum*, *Rubus fruticosus* agg. and *Hyacinthoides non-scripta*.



3.2.3.2 Trampling treatments and timing

3.2.3.2.1 One seasons short-duration trampling and one to two years recovery

In each of the four replicate sets of trampling lanes, one control lane received no trampling and the remaining lanes received either 5, 25, 75, 200 or 500 passes. The range of 0 to 500 passes accurately gauges vegetation response in the sampled

vegetation types, because the number of passes required to reduce cover by 50 % (a key level of response in this method) was within the specified range. The experimental levels were also representative of actual seasonal visitor numbers recorded along trails (Chapter 2).

A single pass consisted of a uni-directional walk at a natural gait through the lane. Passes were spread evenly over the entire lane area by randomly staggering starts across the lane width. Turning occurred outside of the trampling lanes and plots were trampled all on the same day for all treatments and replications. In all instances, the fieldwalker weighed 90 kg and wore lug-soled boots. Treatments were administered in dry weather when vegetation cover was at a maximum but some of the growing season still remained. Consequently, stands of coniferous and deciduous *Hyacinthoides non-scripta* were sampled in April 1995, the *Pteridium aquilinum* stand in June 1995 and the *Rubus fruticosus* agg. stand in July 1996. Follow up measurements were made exactly one year later in all vegetation types, and two years later for half the replicate sets in stands dominated by *Pteridium aquilinum* and *Hyacinthoides non-scripta* (deciduous) only.

3.2.3.2.2 Two seasons' short-duration trampling and one years recovery

A further season's trampling was applied to two of the four replicate sets of experimental trampling lanes in the *Hyacinthoides non-scripta* (deciduous) and *Pteridium aquilinum* stand types. The range of 5, 25, 75, 200 and 500 trampling passes were repeated for a second time in the same lanes as before. Treatments were administered in April 1996 for *Hyacinthoides non-scripta* and in June 1996 for *Pteridium aquilinum*. Follow up measurements were made one year later.

3.2.3.2.3 One season's long-duration trampling and one years recovery

Treatments of 5, 25, 75, 200 and 500 passes were spread out over a ten week period in the *Hyacinthoides non-scripta* (deciduous) stand. Treatments were made between

February 1995 and April 1995 on vegetation located adjacent to the stands sampled in the short-duration trampling study. Trampling treatments were as follows:

- 5 passes - 1 pass every 2 weeks
- 25 passes - 2 passes weeks 1 to 6; 3 passes, weeks 7 to 9; 4 passes week 10
- 75 passes - 7 passes, weeks 1 to 5; 8 passes, weeks 6 to 10
- 200 passes - 20 passes, weeks 1 to 10
- 500 passes - 50 passes, weeks 1 to 10

Follow up measurements were made exactly one year later.

3.2.3.3 *Measurements*

Two adjacent 30 cm by 50 cm subplot quadrats were placed in each lane (Fig. 3.1), and the following parameters were measured in all four vegetation types (unless otherwise stated):

- Visual estimates of the percentage cover of all living vascular plant and moss species. Cover was recorded as zero if there was no cover and '+' if cover was less than 0.5 %.
- Visual estimates of the cover of bare ground (ground not covered by live vegetation) including exposed organic and humic soil, leaf litter and litter of recently trampled plants.
- Estimates of vegetation height using a point quadrat frame with pins set at 5 cm intervals. The frame was placed a total of five times at systematic intervals along the length of each subplot, giving 25 replications per subplot. When the pins were dropped, stature was estimated to the nearest centimetre if the pin struck live vegetation, and a zero was recorded if bare ground was hit.
- Harvests of above ground leaf biomass and the corresponding leaf areas for coniferous and deciduous *Hyacinthoides non-scripta* stands only. Living plant matter was collected from *outside* the subplots but still within the perimeter of the lane so as to not adversely effect the other measured variables. Leaf area per leaf was measured on each of 50 harvested leaves (where available) by using a CI-202 scanning area

meter (CID inc.; available from ELE International, Hemel Hempstead, Herts.). Dry leaf biomass was calculated by oven-drying samples at 110 °C overnight, and reweighing the dried samples.

- Soil compaction was determined by measuring surface soil penetrative resistance using a hand held penetrometer in the *Hyacinthoides non-scripta* (deciduous) stand only. Five random measurements were made in each subplot and a mean soil penetrative resistance per subplot in 'kg / cm²' was obtained.
- The response of flowering and seeding of the *Hyacinthoides non-scripta* stand was gauged by measuring the following flowering and seeding variables in each subplot:

Flowering data:

- Total number of flowering scapes per subplot (0.15 m²)
- Average flowering scape height (cm)
- Average number of flowers per scape
- Total number of flowers per subplot (0.15 m²)

Seeding data:

- Total number of seeding scapes per subplot (0.15 m²)
- Average seeding scape height (cm)
- Average number of capsules per scape
- Total number of capsules per subplot (0.15 m²)
- Average number of seeds per capsule
- Average number of seeds per scape
- Total number of seeds per subplot (0.15 m²)

A complete set of initial measurements were made immediately before trampling on both subplots in each lane. Height and soil penetrative resistance measurements were made directly after trampling, and subplots were re-assessed for vegetation and bare ground cover approximately two weeks after trampling. Flowering data was estimated six weeks after trampling, and seed data was collected ten weeks after trampling.

Scapes were harvested at ground level from each subplot to allow accurate seed counts.

Follow-up measurements after one or two years recovery, and a second seasons trampling were made where specified in the different individual investigations.

3.2.4 *Analysis of results*

3.2.4.1 *Data analysis*

Changes in edaphic and vegetation characteristics caused by trampling are expressed as a proportion of the original conditions, adjusted by using a correction factor (*cf*) to account for variations on the control plots (Bayfield 1979a, Cole 1985, Cole & Bayfield 1993). The indicators of ecosystem change are as follows:

3.2.4.1.1 Relative cover for individual species and the vegetation type

Vegetation cover is expressed as the total sum of all cover values of all species for the vegetation type, and accounts for overlapping vegetation. The total cover values are summed for each subplot (a '+' was given a nominal value of 0.2 %) and pooled with the other subplot in each lane to derive a mean total cover value that avoids pseudoreplication (Cole 1995b). The relative cover (*RC*) is a measure of the percent fraction of original vegetation that survives trampling, adjusted for changes on controls. It is calculated using the following equation:

$$RC = \frac{\text{surviving cover on trampled subplots}}{\text{initial cover on trampled subplots}} \times cf \times 100\%$$

$$\text{where } cf = \frac{\text{initial cover on control subplots}}{\text{surviving cover on control subplots}}$$

Relative cover after one or two seasons trampling, and after one or two years recovery was calculated for each trampling treatment in each vegetation type (where applicable).

The vegetation types are dominated by almost continuous monocultures of the dominant species, so a second relative cover measure equation is used to more accurately gauge the response of individual species:

$$RC = \frac{\text{surviving cover on trampled subplots}}{\text{initial cover on trampled subplots} - cf} \times 100\%$$

where $cf =$ (initial cover on control subplots - surviving cover on control subplots)

This second relative cover measure utilises a correction factor based on absolute values rather than proportional differences on the control. It yields similar results to the first equation as long as control lanes are similar pre- and post-treatment, and that species are present on most plots (Cole & Bayfield 1993).

Relative cover values would equal 100 % in the absence of any change in cover caused by trampling. Hence, the extent to which the relative cover deviate from 100 % gives an indication of the damage caused by trampling, and allows the overall vegetation vulnerability to be classified using three main 'durability indices' (section 3.2.4.2).

3.2.4.1.2 Relative height of the vegetation type

Height data in each subplot was pooled (a '+' value was given a nominal value of 0.2 cm), and the mean height obtained by dividing the total by the number of non-zero values. The mean height of the two subplots derived the mean vegetation height. Relative height was calculated by substituting mean height values for mean cover values in the first equation given in section 3.2.4.1.1. Relative height after one or two seasons trampling, and after one or two years recovery was calculated for each trampling treatment in each vegetation type (where applicable).

3.2.4.1.3 Relative leaf area, biomass and seed and flowering data for *Hyacinthoides non-scripta*

Mean leaf area was derived by dividing the total (in cm²) by the number of samples in each lane. The mean leaf area was converted to relative leaf area by substituting mean cover values for mean leaf area values in the first equation given in section 3.2.4.1.1. Relative leaf area after one or two seasons trampling, and after one or two years recovery was computed. Relative biomass and relative seeding and flowering characteristics were estimated using the same method.

3.2.4.1.4 Bare ground and soil penetrative resistance

Bare ground values were simply descriptive measures of changes in ground cover that resulted from trampling impacts. Unlike previous data sets, bare ground estimates were not adjusted for changes on controls because the amount of exposed bare ground on controls ^{was} negligible. Mean values were calculated for each trampling intensity between 0 and 500 passes in each of the vegetation types.

The surface soil penetrative resistance for sandy-loam soils of Tocil Wood were also estimated. Changes in soil compaction were inferred by comparing trampled lanes to control lanes, and soil penetrative resistance (*SPR*) was calculated as:

$$\text{Increase in } SPR = (SPR \text{ on trampled subplots} - SPR \text{ on control})$$

Bare ground and increases in soil *SPR* after one or two seasons trampling, and after one or two years recovery, were calculated for each trampling treatment in each vegetation type (where applicable).

3.2.4.2 Durability Indices

The vulnerability of the varying facets of each vegetation type were characterised by generating resistance, resilience and tolerance indices. Relationships between mean relative parameter (*Y* axis) and amount of trampling (*X* axis) were investigated by constructing scatterplots to illustrate the impact after one to two seasons trampling, and after one to two years recovery.

The 'index of resistance' was the mean relative parameter (*Y* axis) from 0 to 500 passes. It was equivalent to the proportional area below the interpolated curve that equated trampling intensity to relative parameter after trampling had occurred. First defined by Cole (1985), it was estimated by dividing the area beneath the curve on the scatterplot by the total area of the graph. Liddle (1975a) suggested that an indicator of resistance can be based on the number of passes that reduced the relative value by 50 %. Thus a second measure of resistance was defined as the minimum number of passes that caused a 50 % relative loss.

The index of resilience indicated how much recovery had occurred over the year. Resilience was obtained by subtracting the mean relative value after trampling from that after one or two years recovery. This value was divided by 100 % and approximated the optimal amount of recovery that occurred. A second measure was proposed by Cole & Bayfield (1993), which was the change in ^{the} relative parameter one year later following a 50 % reduction in value caused by trampling. This was delineated as a percent of the vegetation change caused by trampling (a 50 % loss).

The index of tolerance was the mean relative parameter (*Y* axis) from 0 to 500 passes after one or two years of recovery. It was estimated in the same way as for the resistance index, but was based on the one or two years recovery curve. A second measure of tolerance was defined by Cole & Bayfield (1993) as the number of passes a vegetation type will tolerate and retain a relative value of at least 75 % one year after trampling.

In summary, indices of resistance, resilience and tolerance are calculated as:

- a). *Index of resistance:*
 - The mean relative parameter value after 0 to 500 passes
 - The minimum number of passes that causes a 50 % relative parameter value loss
- b). *Index of resilience:*
 - The mean increase in ^{the} relative parameter value one year after 0 to 500 passes, as a percent of the damage caused by trampling

- The percent increase in relative parameter value one year after a 50 % loss
- c). *Index of Tolerance:*
 - The mean relative parameter value one year after 0 to 500 passes
 - The maximum number of passes that leaves at least 75 % relative parameter value one year after trampling

(After Cole & Bayfield 1993)

Various indices were proposed:

- *Primary Indices* One seasons trampling and one years recovery
- *Secondary Indices* One seasons trampling and two years recovery
- *Tertiary Indices* Two seasons trampling and one years recovery

3.2.5 Statistical analysis

Statistical analysis was performed using SYSTAT 5.2.1. One- and two-way analysis of variance tested for significant differences between trampling treatments and vegetation types. Data sets were ranked and Liliefors test ensured the normal distribution of samples. The multiple comparison Tukey 'honestly significant difference' test identified significant differences between trampling treatments and vegetation types. Linear and curvi-linear (second order polynomial) regression models were calculated to approximate the relationship between trampling intensity and vegetation response. Some of the data sets were $\log_{(10)}$ or $(X = X^2)$ transformed to conform to the assumptions of homoscedasticity and normality with regard to the values of the dependent variable (Zar 1984).

Chapter 3

PART ONE

The impact of short-duration experimental trampling on vegetation and soils characteristic of ground flora dominated by *Pteridium aquilinum*, *Rubus fruticosus* agg. and *Hyacinthoides non-scripta*.

3.3 Results

3.3.1 Vegetation cover

All pre-treatment stands in the *Pteridium aquilinum*, *Rubus fruticosus* agg. and *Hyacinthoides non-scripta* (deciduous) stands are densely vegetated and species poor (Table 3.2).

Table 3.2 - Pre-treatment mean percent cover and frequency before trampling of all species in each of the four vegetation types

Species	Vegetation type ^a							
	HN		hn		RF		PA	
	F% ^b	C% ^c	F%	C%	F%	C%	F%	C%
<i>Hyacinthoides non-scripta</i>	100	79	100	45				
<i>Holcus mollis</i>	7	13						
<i>Rubus fruticosus</i> agg.	22	12	10	6	100	90	12	8
Moss spp.	7	8						
<i>Anemone nemorosa</i>	7	3	4	3				
<i>Galium aparine</i>	2	2						
<i>Acer pseudoplatanus</i> ^d	35	0.3					10	0.2
<i>Digitalis purpurea</i>			6	9				
<i>Dryopteris filix-mas</i>					4	11		
<i>Lonicera periclymenum</i>					4	8		
<i>Pteridium aquilinum</i>							100	80
<i>Galeobdolon luteum</i>							2	9

^a - HN = *Hyacinthoides non-scripta* (deciduous); hn = *Hyacinthoides non-scripta* (coniferous); RF = *Rubus fruticosus* agg. ; PA = *Pteridium aquilinum*

^b - F% = the percentage proportion of the 48 subplots in which the species was found

^c - C% = mean percent cover

^d - tree seedling

3.3.1.1 After one seasons trampling and one and two years recovery

Vegetation cover differs significantly with the number of passes and the vegetation type both after and one year after trampling (Table 3.3). The significant interaction between the two factors means the effect of the vegetation type is not independent of

the presence of a particular level of trampling intensity. The differences one year after trampling are lower in magnitude than those two weeks after trampling.

Table 3.3 - Ranked two-way ANOVA and Tukey multiple comparisons for relative cover after trampling and after 1 years recovery for the four vegetation types.

Source	After trampling			After 1 year		
	df	F	p	df	F	p
Number of passes	4	166.2	>0.0001	4	60.3	>0.0001
Vegetation type	3	241.9	>0.0001	3	33.9	>0.0001
Interaction	12	10.5	>0.0001	12	3.4	0.0002
Significantly Different Treatments^a						
Number of passes	(5>25>75>200>500)			(5,25)>75>(200,500)		
Vegetation types ^b	(HN,hn)>RF>PA)			(RF,PA)>(HN,hn)		

^a - significant at $p \leq 0.001$

^b - HN = *Hyacinthoides non-scripta* (deciduous); hn = *Hyacinthoides non-scripta* (coniferous); RF = *Rubus fruticosus* agg; PA = *Pteridium aquilinum*

In all the vegetation types, relative cover decreases with each successive increase in the number of passes (Fig. 3.2). Loss in vegetation cover is most pronounced in the *Pteridium aquilinum* stand, where a 50 % cover loss occurs after just 20 passes and all live vegetation is eliminated between 75 and 200 passes. The *Rubus fruticosus* agg. stand undergoes a 50 % cover loss after 120 passes, and both *Hyacinthoides non-scripta* stands are significantly more resistant than either of the other vegetation types (Plate 3.5a). Indeed, the deciduous stand undergoes a 50 % cover loss after 380 passes, and the coniferous stand a 50 % loss after 170 passes. This indicates that response appears to be more resistant in the partially shaded deciduous sub-community. Differences amongst the range of trampling treatments (0 to 500 passes) are significant after trampling.

Mean relative vegetation cover increases substantially from zero percent cover after 500 passes to 75 % and 74 % one year later in the *Pteridium aquilinum* and *Rubus fruticosus* agg. stands respectively. In both of these stand types, recovery is significantly more rapid than the negative rates recorded in deciduous and coniferous

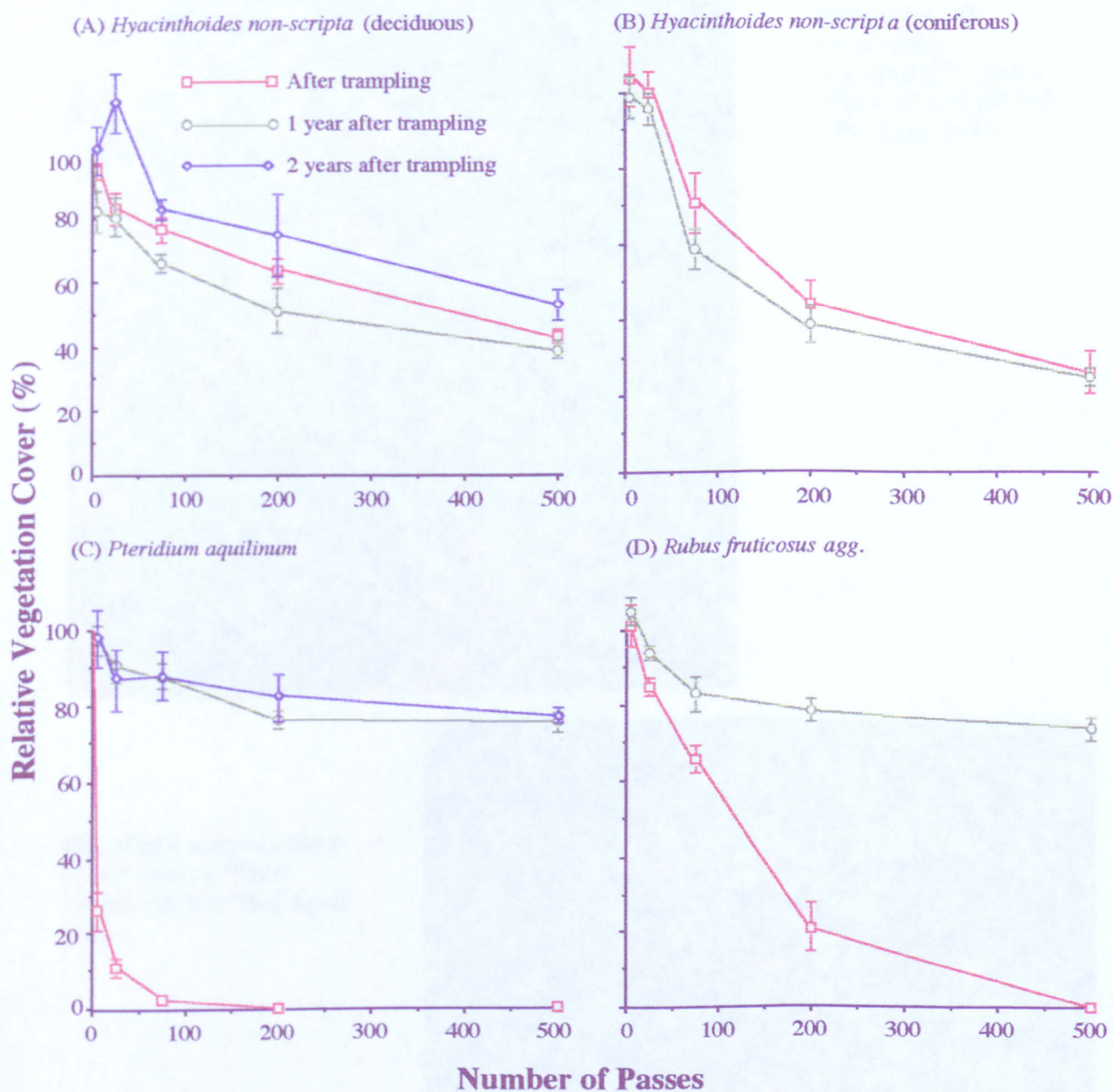


Fig. 3.2 - Relative vegetation cover after trampling and after one and two (A) and (C) only) years of recovery in four vegetation types. Vertical bars show one standard error above and below the mean.



Plate 3.5 -
Hyacinthoides non-
scripta (deciduous)
 dominated sub-
 community,
 (a). after 200 passes
 (Tocil Wood; SP 303
 754, April 1995)

(b). after a second season
 of 500 passes (Tocil
 Wood; SP 303 754, April
 1996)



Hyacinthoides non-scripta stands. Indeed, the relative cover values directly after 500 passes decline from 43 % to 38 % in the deciduous stand and 26 % to 25 % in the coniferous stand. The overall magnitude of differences between levels of trampling intensity are lower one year after trampling than directly after trampling.

After two years, recovery of the *Hyacinthoides non-scripta* stand (deciduous) is far more favourable. There is an increase of 14 % in mean relative vegetation cover from the first year of recovery to 52 % in the 500 pass lane. In addition, there is a minor increase of 2 % from a first year of recovery to a second at 77 % in the *Pteridium aquilinum* stand. Recovery in the *Pteridium aquilinum* stand is so profound that after two years of recovery there are no significant differences between treatment lanes(Table 3.4).

Table 3.4 - Ranked one-way ANOVA and Tukey multiple comparisons for relative cover and height after two years recovery for two vegetation types.

Source	After 2 years					
	Cover			Height		
	df	F	p	df	F	p
HN ^a	39	9.3	0.0005	9	5.4	0.0464
PA	39	1.4	0.292	39	40.0	0.0005
Significantly Different Treatments ^b (Number of Passes)						
HN	(5,25,75,200)>500; 25>200			5>500		
PA	NS			(5,25,75)≥(200,500); 75,200		

^a - HN = *Hyacinthoides non-scripta* (deciduous); PA = *Pteridium aquilinum*

^b - significant at $p \leq 0.05$; NS = non-significant

The linear and curvilinear regression models approximate the relationship between relative vegetation cover and trampling intensity (Table 3.5). In all four vegetation types after, one year after and two years after trampling the polynomial models provide a marginally more favourable fit to the data than the linear models, but approximations are often very similar.

Table 3.5 - Polynomial (second-order) regression models that approximate the relationship between short- and long-duration trampling intensity ($X = 0$ to 500 passes) and relative vegetation cover after, 1 and 2 years after, after a second season and 1 years recovery after trampling for four vegetation types. Linear regression coefficients of determination (r^2) are also provided.

Vegetation Type	Regression Model	Polynomial r^2	Linear r^2
<i>Hyacinthoides non-scripta</i> (deciduous)			
After 1st	$Y = 94.5 - 0.21x + 0.00022x^2$	0.958	0.893
1 year	$Y = 89.7 - 0.28x + 0.00036x^2$	0.929	0.781
2 years	$Y = 105.5 - 0.20x + 0.00019x^2$	0.863	0.823
After 2nd	$Y = 102.3 - 0.32x + 0.00030x^2$	0.998	0.955
1 year	$Y = 104.9 - 0.33x + 0.00039x^2$	0.981	0.865
<i>Hyacinthoides non-scripta</i> (coniferous)			
After	$Y = 104.1 - 0.41x + 0.00051x^2$	0.983	0.848
1 year	$Y = 100.4 - 0.45x + 0.00060x^2$	0.967	0.777
<i>Rubus fruticosus</i> agg.			
After	$Y = 100.8 - 0.53x + 0.00066x^2$	0.998	0.859
1 year	$Y = 100.5 - 0.18x + 0.00025x^2$	0.902	0.674
<i>Pteridium aquilinum</i>			
After 1st ^a	$Y = 1.83 - 0.041x + 0.0003x^2$	0.939	0.865
1 year	$Y = 97.9 - 0.15x + 0.00012x^2$	0.969	0.719
2 years	$Y = 96.3 - 0.11x + 0.00013x^2$	0.831	0.698
After 2nd	$Y = 1.54 - 0.013x + 0.00002x^2$	0.872	0.549
1 year ^a	$Y = 98.8 - 0.16x + 0.00021x^2$	0.996	0.844
<i>Hyacinthoides non-scripta</i> (long-duration trampling; deciduous)			
After	$Y = 99.7 - 0.29x + 0.0003x^2$	1.000	0.940
1 year	$Y = 98.4 - 0.36x + 0.0004x^2$	0.982	0.861

^a - Relative cover \log_{10} transformed

In all cases the second-order polynomial regression model fits the following quadratic equation to the data:

$$Y = a - bX + cX^2$$

where 'Y' is relative vegetation cover, 'X' is the number of passes, 'a' is a constant and 'b' and 'c' are slope coefficients.

3.3.1.2 After two seasons trampling and one years recovery

Vegetation cover differs significantly with the number of passes after a second seasons trampling and with a subsequent years recovery (Table 3.6). In the *Pteridium aquilinum* stand, differences one year after trampling are lower in magnitude than after trampling, but vice-versa in the *Hyacinthoides non-scripta* (deciduous) stand.

Table 3.6 - Ranked one-way ANOVA and Tukey multiple comparisons for relative cover after a second seasons trampling and a subsequent years recovery for two vegetation types.

Source	After 2nd season			After 1 year		
	df	F	p	df	F	p
HN ^a	19	14.8	<0.0001	19	21.1	<0.0001
PA	19	32.3	<0.0001	19	10.8	0.0003
Significantly Different Treatments ^b (Number of Passes)						
HN	(5,25,75)≥(200,500); 75,200			(5,25)>(75,200)>500		
PA	(5,25)>75>(200,500)			(5,25,75)≥(200,500); 75,200		

^a - HN = *Hyacinthoides non-scripta* (deciduous); PA = *Pteridium aquilinum*

^b - significant at $p \leq 0.05$; NS = non-significant

The pattern of vegetation response after a second seasons trampling is identical to the first, but loss in cover is more rapid following the application of a further seasons trampling than just one season in both vegetation types (Fig. 3.3). For instance, the *Pteridium aquilinum* stand undergoes a 50 % cover loss after just 2 passes! In contrast, the *Hyacinthoides non-scripta* (deciduous) loses 50 % relative cover after 200 passes, with relative cover falling to just 16 % in the 500 pass lane. Additional trampling for a second season in the *Hyacinthoides non-scripta* (deciduous) exposes underlying organic soils (Plate 3.5b). Thus, the cumulative impact of two seasons heavy trampling (500 passes) is drastic, and application of a further 500 passes will probably eliminate vegetation cover completely.

Mean relative cover in both the vegetation types increases after one years recovery. Indeed, the mean relative cover in *Hyacinthoides non-scripta* (deciduous) recovers to 39 % one year after two seasons of 500 passes. Patterns in the *Pteridium aquilinum*

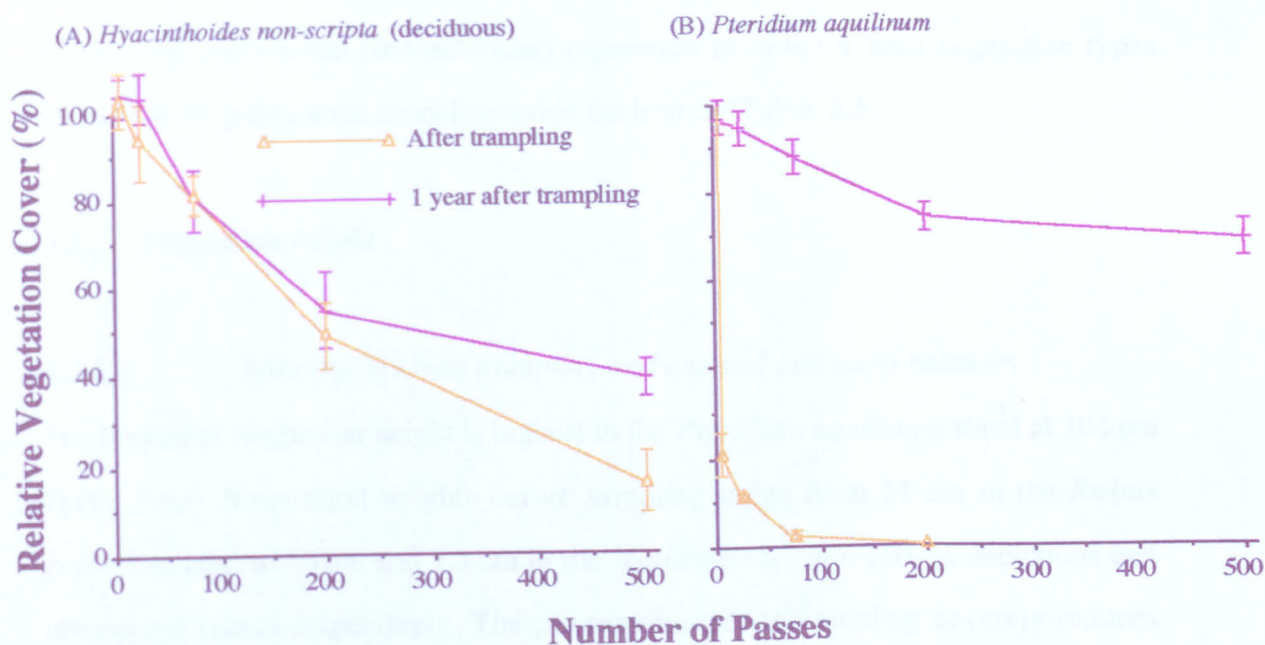


Fig. 3.3 - Relative vegetation cover after a second season of trampling and subsequent recovery after 1 year in two vegetation types. Vertical bars show one standard error above and below the mean.

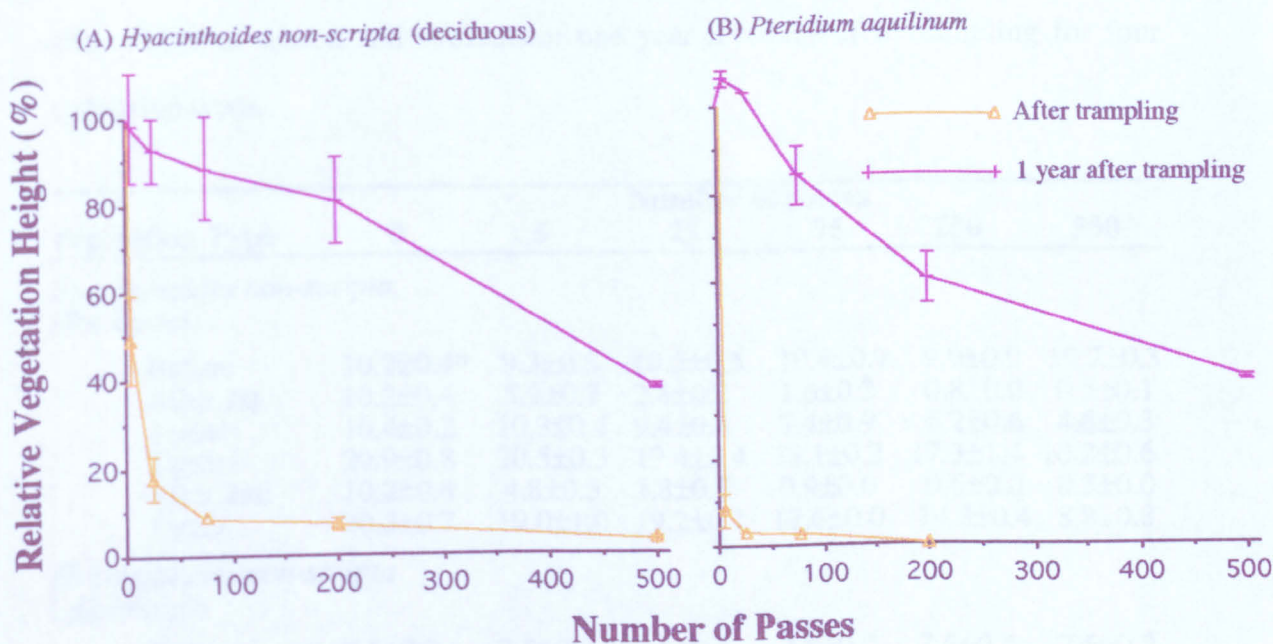


Fig. 3.4 - Relative vegetation height after a second season of trampling and subsequent recovery after 1 year in two vegetation types. Vertical bars show one standard error above and below the mean.

stand are similar, with a relative drop in cover of 6 % to 69 % compared to the relative cover after one season.

Linear and polynomial (second-order) regression models for both vegetation types show that the polynomial models provide the best fit (Table. 3.5).

3.3.2 Vegetation height

3.3.2.1 After one seasons trampling and one and two years recovery

Pre-treatment vegetation height is highest in the *Pteridium aquilinum* stand at 104 cm (Plate 3.6a). Vegetation heights before sampling range from 34 cm in the *Rubus fruticosus* agg. to 10 cm and 7.5 cm in the *Hyacinthoides non-scripta* deciduous and coniferous stands respectively. The physical impact of trampling severely reduces vegetation height in all four vegetation types (Table 3.7).

Table 3.7 - Mean vegetation height (cm) before, after, after 1 and 2 years recovery, after a second season and subsequent one year recovery after trampling for four vegetation types.

Vegetation Type	Number of passes					
	0	5	25	75	200	500
<i>Hyacinthoides non-scripta</i> (deciduous)						
Before	10.2±0.4 ^a	9.3±0.5	10.5±0.5	10.4±0.7	9.9±0.9	10.7±0.3
After 1st	10.2±0.4	5.9±0.7	2.8±0.2	1.6±0.2	0.8±0.0	0.5±0.1
1 year	10.4±0.2	10.3±0.4	9.4±0.4	7.4±0.9	6.2±0.6	4.6±0.3
2 years	20.9±0.8	20.5±0.3	19.4±0.4	18.1±0.2	17.3±1.4	10.2±0.6
After 2nd	10.2±0.4	4.8±0.5	1.8±0.5	0.9±0.0	0.6±0.0	0.3±0.0
1 year	20.3±0.7	19.0±1.0	19.2±0.1	17.6±0.0	14.3±0.4	8.8±0.8
<i>Hyacinthoides non-scripta</i> (coniferous)						
Before	7.5±0.2	7.5±0.3	7.3±0.4	7.5±0.2	7.5±0.4	7.5±0.2
After	7.5±0.2	3.7±0.2	1.9±0.1	1.0±0.1	0.6±0.0	0.2±0.0
1 year	8.0±0.1	7.8±0.4	7.2±0.4	5.8±0.1	4.8±0.4	3.5±0.2
<i>Rubus fruticosus</i> agg.						
Before	34.0±1.8	34.9±1.7	33.9±3.0	33.8±2.6	32.2±1.3	34.2±2.0
After	34.6±1.3	19.2±0.4	12.7±0.7	6.7±0.4	3.2±0.5	0.2±0.1
1 year	34.4±1.1	35.2±1.4	31.2±2.2	29.8±2.3	30.0±3.2	17.4±1.0



Plate 3.6 - *Pteridium aquilinum* dominated sub-community;
(a). before the first treatment

(b). after 25 passes (Tocil Wood; SP 303 754, June 1996)



Vegetation Type	Number of passes					
	0	5	25	75	200	500
<i>Pteridium aquilinum</i>						
Before	103.9±2.0	102.6±2.1	92.8±3.9	100.7±2.8	89.5±2.1	—
After 1st	148.0±2.8	22.1±1.9	6.9±0.7	4.6±0.4	—	—
1 year	150.4±2.0	142.2±2.2	146.9±1.9	106.0±3.3	79.2±2.1	71.9±2.1
2 years	163.5±7.0	156.7±6.6	145.0±4.0	129.2±5.0	83.2±2.7	63.7±2.4
After 2nd	148.7±3.6	21.2±4.3	12.5±1.4	2.7±1.3	—	—
1 year	150.7±3.6	152.7±3.7	145.2±2.4	124.5±4.7	73.0±1.2	52.5±3.2

^a - one standard error above and below the mean

The response of vegetation height differs significantly with the vegetation type and the trampling intensity (Table. 3.8), and the interaction between these two factors is also significant. Loss in relative vegetation height is greatest in the *Pteridium aquilinum* stand, where just 5 passes reduce the relative height to 15 % (Fig. 3.5). The response of vegetation height to trampling is similar amongst the other three vegetation types. The entire range of trampling treatments (0 to 500 passes) differ significantly in relative height after trampling as a combination of all four vegetation types, we combined.

Table 3.8 - Ranked two-way ANOVA and Tukey multiple comparisons for relative height after trampling and after 1 years recovery for the four vegetation types.

Source	After trampling			After 1 year		
	df	F	p	df	F	p
Number of passes	4	383.9	>0.0001	4	96.0	>0.0001
Vegetation type	3	218.0	>0.0001	3	6.5	0.00067
Interaction	12	7.4	>0.0001	12	3.9	0.00022
Significantly Different Treatments^a						
Number of passes	(5>25>75>200>500)			(5,25)>(75,200)>500		
Vegetation types ^b	(HN,hn,RF>PA)			(RF>HN,hn),PA)		

^a - significant at $p \leq 0.001$

^b - HN = *Hyacinthoides non-scripta* (deciduous); hn = *Hyacinthoides non-scripta* (coniferous); RF = *Rubus fruticosus* agg. ; PA = *Pteridium aquilinum*

After 200 passes, the *Rubus fruticosus* agg. stand recovers from 10 % relative height after trampling to 92 % one year later. This gain in height is significantly greater than

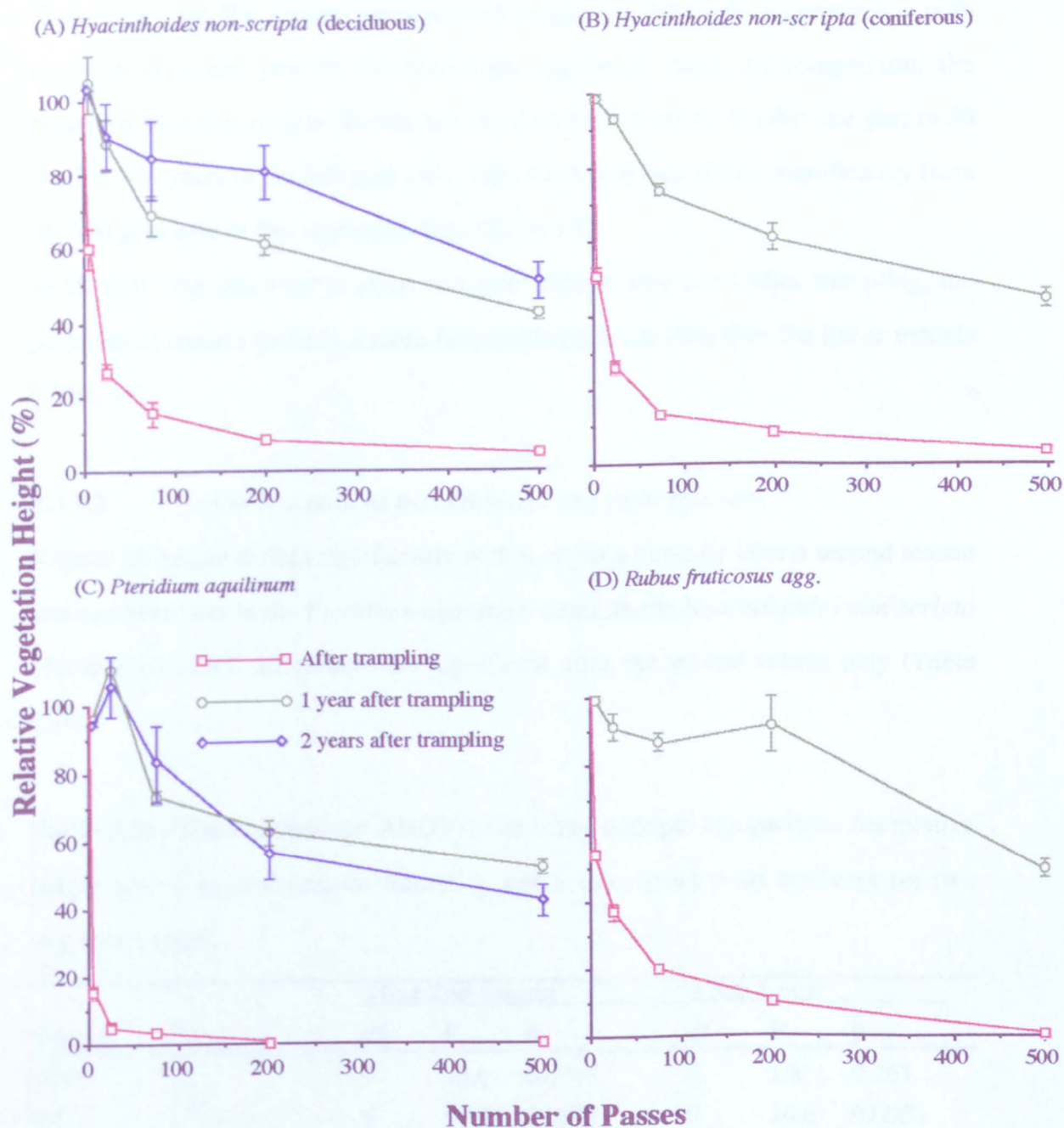


Fig. 3.5 - Relative vegetation height after trampling and after one and two (A) and (C) only) years of recovery in four vegetation types. Vertical bars show one standard error above and below the mean.

all the other stand types, but *Pteridium aquilinum* has the highest mean relative height of 52 % one year after 500 passes.

Two years after 500 passes, mean relative height falls by 10 % in comparison with recovery after one year in the *Pteridium aquilinum* stand. In comparison, the *Hyacinthoides non-scripta* (deciduous) stand recovers from 42 % after one year to 50 % after two years in the 500 pass lane. Only the 5 pass lane differs significantly from the 500 pass lane in this vegetation type (Table 3.4).

In all four vegetation types after, one year after or two years after trampling, the polynomial models provide a more favourable fit to the data than the linear models (Table 3.9).

3.3.2.2 After two seasons trampling and one years recovery

Vegetation height differs significantly with trampling intensity after a second season and one year later in the *Pteridium aquilinum* stand. In the *Hyacinthoides non-scripta* (deciduous) stand, differences are significant after the second season only (Table 3.10).

Table 3.10 - Ranked one-way ANOVA and tukey multiple comparisons for relative height after a second seasons trampling and a subsequent years recovery for two vegetation types.

Source	After 2nd season			After 1 year		
	df	F	p	df	F	p
HN ^a	9	40.0	0.0005	9	1.8	0.261
PA	9	63.3	0.0002	9	14.6	0.0058
Significantly Different Treatments^b (Number of Passes)						
HN	(5,25)≥(75,200)≥500; 25,75:200,500			NS		
PA	(5,25)>75>(200,500)			(5,25)>(200,500)		

^a - HN = *Hyacinthoides non-scripta* (deciduous); PA = *Pteridium aquilinum*

^b - significant at $p \leq 0.05$; NS = non-significant

Table 3.9 - Polynomial (second-order) regression models that approximate the relationship between short and long-duration trampling intensity ($X = 0$ to 500 passes) and relative vegetation height after, 1 year after and 2 years after trampling for four vegetation types. Linear regression coefficients of determination (r^2) are also provided.

Vegetation Type	Regression Model	Polynomial r^2	Linear r^2
<i>Hyacinthoides non-scripta</i> (deciduous)			
After 1st	$Y = 65.9 - 0.52x + 0.00080x^2$	0.662	0.396
1 year	$Y = 98.9 - 0.29x + 0.00035x^2$	0.931	0.811
2 years	$Y = 98.2 - 0.12x + 0.00004x^2$	0.943	0.940
After 2nd	$Y = 59.1 - 0.49x + 0.00076x^2$	0.557	0.320
1 year	$Y = 97.2 - 0.074x + 0.00009x^2$	0.990	0.982
<i>Hyacinthoides non-scripta</i> (coniferous)			
After	$Y = 61.9 - 0.49x + 0.00075x^2$	0.615	0.373
1 year	$Y = 98.5 - 0.27x + 0.00032x^2$	0.978	0.863
<i>Rubus fruticosus</i> agg.			
After	$Y = 67.0 - 0.49x + 0.00072x^2$	0.715	0.491
1 year	$Y = 95.9 - 0.014x + 0.00025x^2$	0.931	0.891
<i>Pteridium aquilinum</i>			
After 1st ^a	$Y = 1.40 - 0.011x + 0.00002x^2$	0.789	0.504
1 year	$Y = 102.4 - 0.29x + 0.00037x^2$	0.868	0.719
2 years	$Y = 102.4 - 0.29x + 0.00034x^2$	0.951	0.852
After 2nd ^a	$Y = 1.24 - 0.01x + 0.000016x^2$	0.653	0.401
1 year	$Y = 105.0 - 0.28x + 0.00029x^2$	0.987	0.919
<i>Hyacinthoides non-scripta</i> (long-duration trampling; deciduous)			
After	$Y = 84.9 - 0.43x + 0.0006x^2$	0.913	0.717
1 year	$Y = 100.2 - 0.30x + 0.0004x^2$	0.961	0.786

^a - Relative height \log_{10} transformed

The impact of a second seasons trampling is more severe than the first season (Fig. 3.4). Indeed, five passes reduces relative height to just 8 % in the *Pteridium aquilinum* stand, and a 50 % height loss occurs after 10 passes in the *Hyacinthoides non-scripta* (deciduous) stand.

Relative height in the *Pteridium aquilinum* stand recovers to 38 % one year after two seasons of 500 passes, 14 % lower than that present after one season of disturbance.

In the *Hyacinthoides non-scripta* (deciduous) stand, mean relative height after 500 passes declines to 38 %, 4 % lower than the recovery after one season. The lack of between lane differences are as a consequence of the highest impact being caused by the first season of trampling.

The best approximation of the relationship between trampling intensity and relative height are given by the polynomial regression models (Table 3.9).

3.3.3 Leaf area and biomass

Mean pre-treatment *Hyacinthoides non-scripta* leaf biomass ranges from 0.10 g / leaf in the deciduous stand to 0.06 g / leaf in the coniferous stand. The proportional differences in mean leaf area are similar, with mean leaf sizes of 18.2 cm² and 9.4 cm² in the deciduous and coniferous woodland stands respectively (Table 3.11).

Overall rates of loss in biomass and leaf area are more rapid in the coniferous than in the deciduous stand. For example, relative biomass is 22 % higher and relative leaf area 10 % higher in the latter stand compared to the former after one season of 500 passes. Recovery rates are negative in both stand types after one year, but there is a slightly more favourable recovery two years later, e.g.: increases in relative biomass and leaf area after 500 passes in the deciduous stand of 5 % and 17 % respectively. A second season of trampling reduces relative leaf area to just 15 % after 500 passes, and recovery rates for both relative biomass and leaf area are again negative.

Table 3.11 - Mean leaf area (cm²) and biomass (g) per leaf before, after, 1 and 2 years recovery, a second season and subsequent one year recovery after trampling for two vegetation types.

Vegetation Type	Number of passes					
	0	5	25	75	200	500
Biomass						
<i>Hyacinthoides non-scripta</i> (deciduous)						
Before	0.102	0.105	0.098	0.110	0.102	0.097
After 1st	0.102	0.083	0.073	0.076	0.063	0.040
1 year	0.104	0.079	0.073	0.058	0.043	0.031
2 years	0.103	0.110	0.080	0.071	0.060	0.050
After 2nd	0.093	0.068	0.049	0.047	0.040	0.016
1 year	0.101	0.079	0.065	0.050	0.037	0.020
<i>Hyacinthoides non-scripta</i> (coniferous)						
Before	0.057	0.062	0.056	0.052	0.060	0.054
After	0.060	0.051	0.039	0.032	0.020	0.010
1 year	0.061	0.054	0.030	0.029	0.017	0.009
Leaf Area						
<i>Hyacinthoides non-scripta</i> (deciduous)						
Before	18.01	19.00	17.66	18.09	18.20	18.42
After 1st	18.09	15.01	13.76	11.80	9.10	5.09
1 year	18.85	13.71	14.06	11.36	8.54	3.70
2 years	17.04	16.40	14.80	12.94	9.67	7.00
After 2nd	16.16	14.42	9.33	7.05	5.32	2.11
1 year	19.00	16.10	13.27	10.00	7.54	3.00
<i>Hyacinthoides non-scripta</i> (coniferous)						
Before	9.76	10.13	9.66	9.77	9.69	9.72
After	10.01	8.94	8.00	6.21	4.05	1.77
1 year	9.88	8.04	7.00	5.04	2.84	1.60

The polynomial (second-order) regression models provide a marginally better approximation of the relationship between trampling intensity (0 to 500 passes) and vegetation response than the linear models (Table 3.12).

Table 3.12 - Polynomial (second-order) regression models that approximate the relationship between trampling intensity ($X = 0$ to 500 passes) and relative vegetation biomass and leaf area after, 1 year after and 2 years after trampling for two vegetation types. Linear regression coefficients of determination (r^2) are also provided.

Vegetation Type	Regression Model	Polynomial r^2	Linear r^2
Biomass			
<i>Hyacinthoides non-scripta</i> (deciduous)			
After 1st	$Y = 86.4 - 0.16x + 0.0001x^2$	0.841	0.863
1 year	$Y = 83.4 - 0.33x + 0.0004x^2$	0.861	0.686
2 years	$Y = 91.3 - 0.31x + 0.0004x^2$	0.844	0.831
After 2nd	$Y = 81.4 - 0.27x + 0.0003x^2$	0.808	0.745
1 year	$Y = 84.9 - 0.35x + 0.0005x^2$	0.892	0.742
<i>Hyacinthoides non-scripta</i> (coniferous)			
After	$Y = 86.7 - 0.40x + 0.0005x^2$	0.917	0.754
1 year	$Y = 82.4 - 0.44x + 0.0006x^2$	0.818	0.625
Leaf Area			
<i>Hyacinthoides non-scripta</i> (deciduous)			
After 1st	$Y = 88.5 - 0.27x + 0.0003x^2$	0.931	0.850
1 year	$Y = 82.5 - 0.28x + 0.0003x^2$	0.868	0.799
2 years	$Y = 103.2 - 0.26x + 0.0003x^2$	0.988	0.898
After 2nd	$Y = 90.8 - 0.43x + 0.0006x^2$	0.879	0.727
1 year	$Y = 79.5 - 0.36x + 0.0005x^2$	0.837	0.704
<i>Hyacinthoides non-scripta</i> (coniferous)			
After	$Y = 92.6 - 0.37x + 0.0004x^2$	0.976	0.865
1 year	$Y = 87.4 - 0.43x + 0.0006x^2$	0.944	0.749

3.3.4 Bare ground

Pre-treatment conditions shows that the *Rubus fruticosus* agg. stand has the least visible bare ground at 9.8 %, and the *Hyacinthoides non-scripta* (coniferous) has the most at 64 % (Table 3.13).

Table 3.13 - Mean proportion of bare ground (%) not vegetated before, after, 1 year and 2 years after, after a second season and subsequent one years recovery from trampling for four vegetation types.

Vegetation Type	Number of passes					
	0	5	25	75	200	500
<i>Hyacinthoides non-scripta</i> (deciduous)						
Before	28.2±3.5 ^a	23.7±2.8	25.6±5.5	21.9±3.0	30.8±4.4	25.6±3.2
After 1st	23.0±3.2	27.1±3.4	32.2±4.3	34.7±6.0	47.5±3.7	76.0±4.0
1 year	28.4±4.5	28.3±2.9	35.5±4.0	39.0±3.8	52.0±3.9	79.0±3.8
2 years	22.2±4.4	26.6±3.8	30.9±5.6	31.7±3.4	46.6±4.5	70.7±3.3
After 2nd	25.4±4.6	22.8±5.0	25.9±4.8	32.2±4.5	48.7±5.8	91.0±5.6
1 year	27.3±3.9	24.4±4.5	23.6±3.9	33.8±5.2	51.3±3.6	77.7±5.2
<i>Hyacinthoides non-scripta</i> (coniferous)						
Before	63.7±3.4	56.7±4.5	69.0±3.5	60.6±2.9	70.2±4.5	62.0±3.4
After	58.0±3.0	58.8±4.2	70.9±3.2	73.7±3.4	80.7±4.2	88.8±4.0
1 year	52.5±2.8	56.0±2.9	63.6±2.9	75.0±3.9	82.3±2.1	90.0±5.6
<i>Rubus fruticosus</i> agg.						
Before	8.1±2.5	13.1±3.0	10.6±2.0	8.7±2.8	8.1±2.5	10.0±2.3
After	4.4±2.2	9.4±2.9	21.2±2.3	37.5±4.8	76.9±6.7	100.0±0.0
1 year	5.0±2.1	5.0±1.3	11.9±2.1	20.6±3.5	25.0±2.8	30.6±2.0
<i>Pteridium aquilinum</i>						
Before	30.0±2.8	26.2±4.1	16.2±3.3	17.5±2.3	15.0±2.6	18.1±4.1
After 1st	1.5±1.1	73.1±5.6	86.2±2.8	95.7±0.8	100.0±0.0	100.0±0.0
1 year	1.0±0.2	2.0±0.3	7.2±1.3	9.6±2.1	20.0±2.1	22.3±1.8
2 years	1.0±0.3	1.8±0.2	6.7±1.7	6.0±1.9	16.4±2.2	24.2±2.0
After 2nd	1.2±0.7	78.0±2.1	87.4±2.3	96.0±0.9	100.0±0.0	100.0±0.0
1 year	1.2±0.8	1.5±0.5	6.9±1.4	10.0±2.3	21.0±3.0	28.6±2.6

^a - one standard error above and below the mean

Bare ground is exposed by trampling in all vegetation types. After one year, the *Pteridium aquilinum* stand recovers to be the least visibly barren vegetation type. Erosion of organic horizons commences after approximately 350 passes in the *Hyacinthoides non-scripta* (deciduous) stand, and at lower thresholds in the other vegetation types.

Rates of exposure of bare ground are more rapid after two seasons trampling than after one in the *Pteridium aquilinum* stand, with bare ground decreasing by 5 % to 21 % after 5 passes. Recovery rates after two seasons trampling compare favourably with

rates after one seasons trampling for up to 200 passes in both vegetation types. However, two seasons of greater than 200 passes increase the proportion of ground not covered by live vegetation in *Hyacinthoides non-scripta* (deciduous) stands compared to the impact of one seasons trampling.

Thus, recovery rates appear to be highest in those vegetation types that regain the most cover in the time period after trampling.

3.3.5 *Soil penetrative resistance*

Surface soil compaction increases with each successive rise in the number of passes (Figs. 3.6 & 3.7). Indeed, the curvi-linear relationship with trampling suggests that increases proceed more rapidly at low levels of trampling.

Soil penetrative resistance increases by 1.4 kg cm⁻² after one season of 500 passes. As a total average for all levels of trampling intensity (0 to 500 passes), the increase in soil penetrative resistance declines from 0.6 kg cm⁻² after trampling to 0.2 kg cm⁻² and 0.1 kg cm⁻² after one and two years recovery respectively. At the end of the two year recovery period, soil penetrative resistance in the 500 pass lane is still 1.80 kg cm⁻² higher than control lanes.

After a second season of 500 passes, soil penetrative resistance increases to 3.5 kg cm⁻², 0.8 kg cm⁻² higher than soil conditions after the first season of trampling. As a total average for all levels of trampling (0 to 500 passes), mean soil penetrative resistance decreases from 0.8 kg cm⁻² to 0.5 kg cm⁻² after a subsequent years recovery. Compaction levels are almost identical one year after two seasons trampling to conditions directly after the first seasons trampling in the 500 pass lane.

Curvi-linear models fit the relationship marginally better than alternative linear models for the range of 0 to 500 passes. It is best described by the following polynomial (second-order) quadratic equation:

$$Y = a + b X + c X^2$$

where 'Y' is relative vegetation cover, 'X' is the number of passes, 'a' is a constant and 'b' and 'c' are slope coefficients.

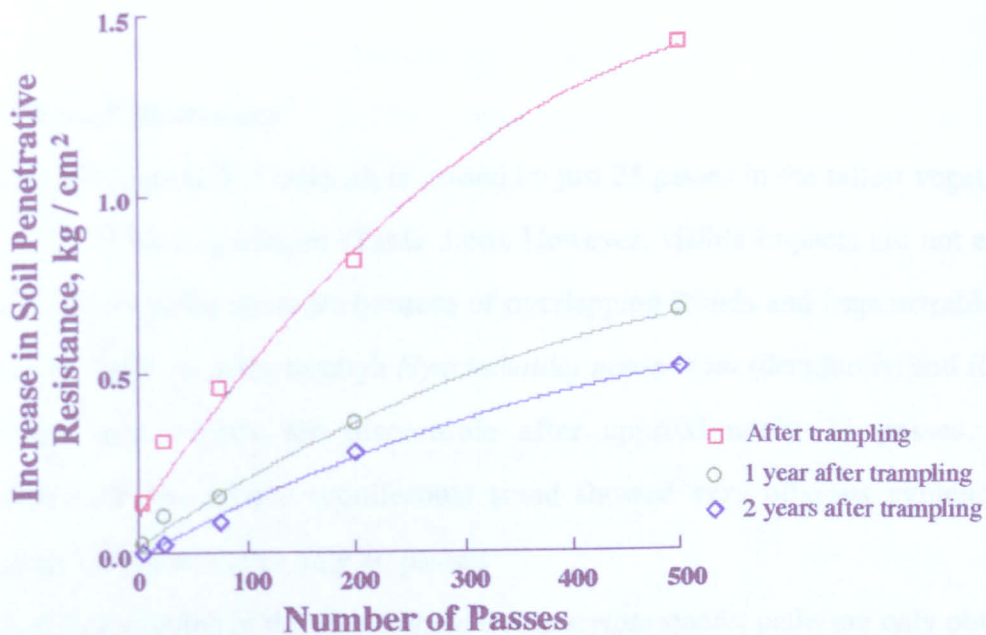


Fig. 3.6 - The relationship between the number of passes and mean increase in soil penetrative resistance after trampling and after one and two years of recovery in the *Hyacinthoides non-scripta* (deciduous). Fitted curves represent second-order polynomial regression models, (after trampling: $Y = 0.104 + 0.004x - 0.000004x^2$; $r^2 = 0.984$; 1 year after trampling: $Y = 0.017 + 0.002x - 0.000001x^2$; $r^2 = 0.995$; 2 years after trampling: $Y = -0.010 + 0.002x - 0.000001x^2$; $r^2 = 0.996$).

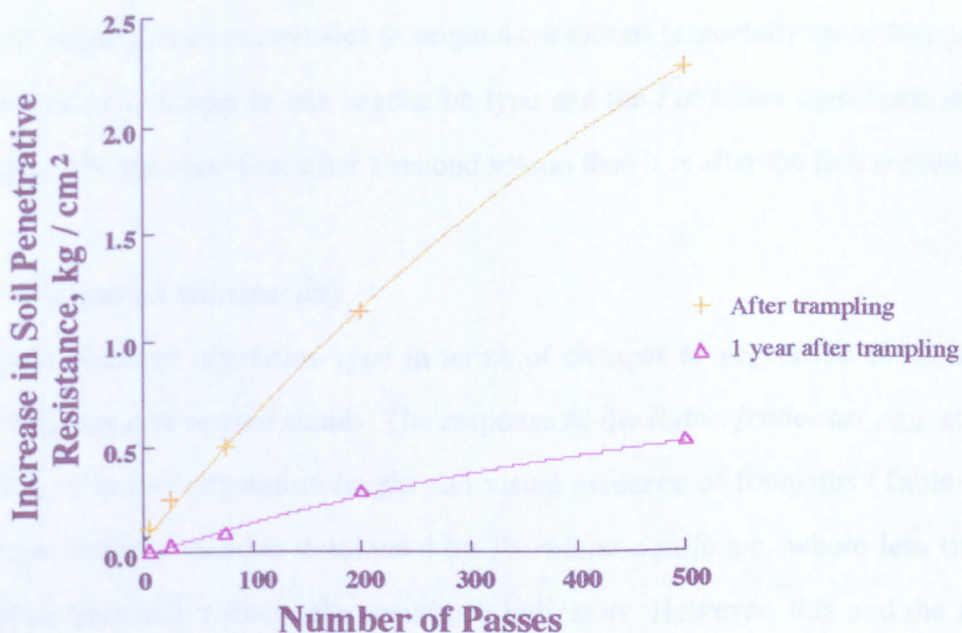


Fig. 3.7 - The relationship between the number of passes and mean increase in soil penetrative resistance after a second season of trampling and after one year of recovery in the *Hyacinthoides non-scripta* (deciduous). Fitted curves represent second-order polynomial regression models, (after trampling: $Y = 0.061 + 0.006x - 0.000003x^2$; $r^2 = 0.998$; 1 year after trampling: $Y = 0.035 + 0.003x - 0.0000004x^2$; $r^2 = 0.996$).

3.3.6 Visual appearance

A clearly distinguishable footpath is caused by just 25 passes in the tallest vegetation stand of *Pteridium aquilinum* (Table 3.6b). However, visible impacts are not easily detected unless paths are wide because of overlapping fronds and impenetrable tall vegetation. Obvious paths through *Hyacinthoides non-scripta* (deciduous) and *Rubus fruticosus* agg. stands are discernible after approximately 75 passes. The *Hyacinthoides non-scripta* (coniferous) stand showed very obvious evidence of trampling disturbance after only 40 passes.

A year after trampling in the *Hyacinthoides non-scripta* stands, paths are only obvious in lanes that receive 200 passes or more. The two other vegetation types recover vegetation cover sufficiently to hide visual evidence of previous use. The obvious reduction in height after 500 passes in the *Pteridium aquilinum* stands is a function of its tall stature, yet a casual observation will probably not elicit an awareness of any appreciable change. The *Rubus fruticosus* agg. stand shows the most similarity in terms of vegetation characteristics to original conditions (especially up to 200 passes). The reduction in height in this vegetation type and the *Pteridium aquilinum* stand is even more obvious one year after a second season than it is after the first season.

3.3.7 Vegetation vulnerability

The most resistant vegetation type in terms of changes to vegetation cover are the *Hyacinthoides non-scripta* stands. The response of the *Rubus fruticosus* agg. stand is similar in terms of vegetation height and visual evidence of footpaths (Table 3.14). The least resistant stand is dominated by *Pteridium aquilinum*, where less than 25 passes substantially reduces the resistance indicators. However, this and the *Rubus fruticosus* agg. stand are highly resilient. Both stands of *Hyacinthoides non-scripta* have negative resiliences one year after trampling in terms of relative cover, but the recovery of the deciduous stand is slightly more favourable. Tolerance indicators in vegetation types are generally higher two years after trampling than one year after.

Resistance and tolerance indicators specific to the two stands of *Hyacinthoides non-scripta* show that the coniferous stand is not only more susceptible to trampling, but is also unable to recover to the same extent as the deciduous stand.

Table 3.14 - First season vegetation type resistance and tolerance (one and two years) for the four vegetation types.

	Vegetation type ^a			
	<i>HN</i>	<i>hn</i>	<i>RF</i>	<i>PA</i>
Resistance indicators				
Relative cover (%)	64	50	30	4
Relative height (%)	12	11	12	1
Relative leaf area (%)	49	42	—	—
Relative biomass (%)	57	36	—	—
Evident path (passes)	75	<75	75	<25
Tolerance indicators (1 year)				
Relative cover (%)	57	43	80	81
Relative height (%)	60	61	78	65
Relative leaf area (%)	41	34	—	—
Relative biomass (%)	43	29	—	—
Evident path (passes)	>200	>75	500	500
Tolerance indicators (2 years)				
Relative cover (%)	73	—	—	84
Relative height (%)	74	—	—	61
Relative leaf area (%)	64	—	—	—
Relative biomass (%)	55	—	—	—
Evident path (passes)	500	—	—	>500

^a - *HN* = *Hyacinthoides non-scripta* (deciduous); *hn* = *Hyacinthoides non-scripta* (coniferous); *RF* = *Rubus fruticosus* agg.; *PA* = *Pteridium aquilinum*

Compared to the first season, a second season of trampling reduces cover resistance in the *Hyacinthoides non-scripta* (deciduous) and *Pteridium aquilinum* stands by 13 %, and 2 % respectively (Table 3.15). The damaging impact of successive seasons of experimental trampling is cumulative, but the first season of trampling has the major impact on tolerance indicators.

Table 3.15 - Second season vegetation type resistance and tolerance for two vegetation types.

	Vegetation type ^a	
	<i>HN</i>	<i>PA</i>
Resistance indicators		
Relative cover (%)	51	2
Relative height (%)	9	1
Relative leaf area (%)	36	—
Relative biomass (%)	42	—
Evident path (passes)	75	5
Tolerance indicators (1 year)		
Relative cover (%)	62	78
Relative height (%)	71	62
Relative leaf area (%)	33	—
Relative biomass (%)	38	—
Evident path (passes)	500	>500

^a - *HN* = *Hyacinthoides non-scripta* (deciduous) & *PA* = *Pteridium aquilinum*

3.3.8 Individual species response

Relative cover and height of the three main species of *Hyacinthoides non-scripta*, *Rubus fruticosus* agg. and *Pteridium aquilinum* are given in Table 3.16. Other species in the vegetation types are too infrequent for reliable estimates to be made. The response of individual species to trampling is similar in all cases to the response of the entire vegetation types (comparing Tables 3.14 and 3.15 to Table 3.16), e.g.: the primary resistance index of *Hyacinthoides non-scripta* (deciduous) stand is 64 %, comparing with 61 % recorded for the individual species. Recovery and tolerance indices follow similar patterns based on one (*primary*) and two (*secondary*) years recovery from one seasons trampling, and on one (*tertiary*) years recovery from two seasons trampling.

Heavy trampling (500 passes) plotted against light trampling (25 passes) after treatments for the major species shows that species are segregated according to their relative cover response (Fig. 3.8). *Hyacinthoides non-scripta* (deciduous) is the most resistant, *Rubus fruticosus* agg. is susceptible to heavy levels of trampling only, whilst *Pteridium aquilinum* is easily damaged by light trampling.

Table 3.16 - Percent durability indices for relative cover based on one year and two years recovery after one and two seasons trampling for the three main species in the four vegetation types studied.

Index ^b	Vegetation Type ^a												
	HN			hn			RF			PA			(HN)
	Pri	Sec	Ter	Pri	Sec	Ter	Pri	Sec	Ter	Pri	Sec	Ter	Pri
Resistance^c													
Mean relative cover after 0 to 500 passes	61.4	—	49.4	48.6	—	—	29.5	—	2.1	2.4	—	2.1	55.0
Minimum no. of passes that caused a 50 % cover loss	380	—	200	170	—	—	120	—	2	20	—	2	250
Resistance Class	m-h	—	m-h	m	—	—	l-m	—	l	l	—	l	m-h
Resilience^d													
Mean increase in cover 1 or 2 years after 0 to 500 passes, as a percent of the damage caused by trampling	-23.8	27.0	19.0	-13.1	—	—	71.4	—	76.9	79.1	82.3	76.9	-13.2
Percent increase in cover 1 or 2 years after 50 % loss	-14.0	20.0	10.0	-12.0	—	—	64.0	—	92.0	90.0	96.0	92.0	-22.0
Resilience Index	l	l	l	l	—	—	m-h	—	h	h	h	h	l
Tolerance^e													
Mean relative cover 1 year or 2 years after 0 to 500 passes	52.2	71.8	59.0	41.9	—	—	79.9	—	77.3	79.6	82.7	77.3	49.0
Maximum no. of passes that leave at least 75 % cover 1 or 2 years after trampling	35	200	105	60	—	—	450	—	200	>500	>500	200	100
Tolerance Index	l	m	m	l	—	—	m-h	—	h	h	h	h	l-m

^a - HN = *Hyacinthoides non-scripta* (deciduous); hn = *Hyacinthoides non-scripta* (coniferous); RF = *Rubus fruticosus* agg.; PA = *Pteridium aquilinum*; (HN) = *Hyacinthoides non-scripta* (long-term trampling; deciduous).

^b - Pri = primary durability indices based on one years recovery; Sec = secondary durability indices based on two years recovery; Ter = tertiary durability indices based on one years recovery from the second season

^c - the minimum number of passes that reduced cover or height by 50 %: h ≥ 500 passes, m = 200 passes, l ≤ 75 passes; h = high, m = moderate, l = low

^d - the recovery after cover was reduced nearly to zero: h = cover ≥ 2/3 of original cover, m = cover between 1/3 and 2/3 of original values, l = cover 1/3 of original cover.

^e - the maximum number of passes that could be tolerated and still possess 75 % of original cover or height: h ≥ 500 passes, m = 200 passes, l ≤ 75 passes.

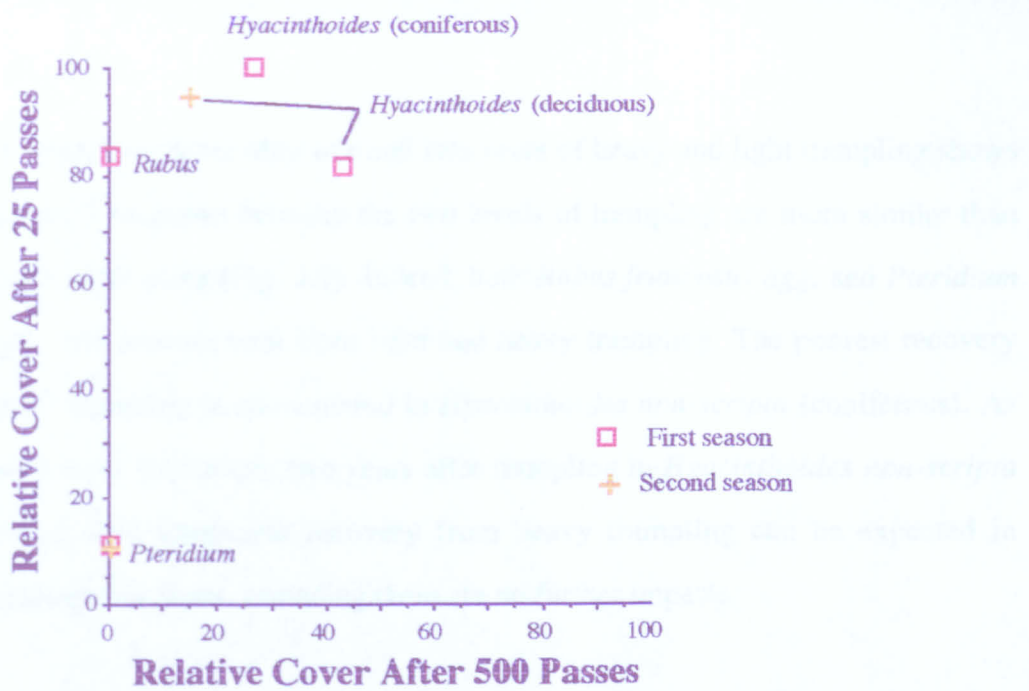


Fig. 3.8 - Relative vegetation cover after light (25 passes) and heavy trampling (500 passes) after one and two season trampling in four vegetation types.

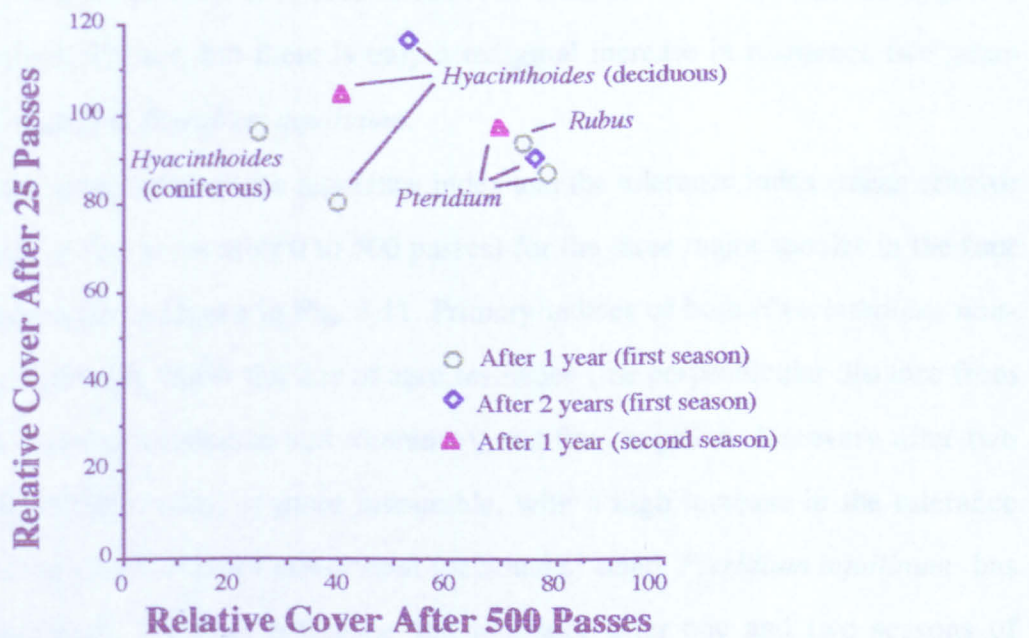


Fig. 3.9 - Relative vegetation cover 1 and 2 years after one and two seasons light (25 passes) and heavy trampling (500 passes) in four vegetation types.

Relative vegetation cover after one and two years of heavy and light trampling shows that vegetation response between the two levels of trampling are more similar than directly after trampling (Fig. 3.9). Indeed, both *Rubus fruticosus* agg. and *Pteridium aquilinum* can recover well from light and heavy trampling. The poorest recovery from heavy trampling is encountered in *Hyacinthoides non-scripta* (coniferous). As response is more favourable two years after trampling in *Hyacinthoides non-scripta* (deciduous), then long-term recovery from heavy trampling can be expected in approximately five years, providing there are no further impacts.

3.3.9 Relationship between resistance, resilience and tolerance

Fig. 3.10 shows the resilience index (mean increase in relative cover one or two years after one or two seasons of 0 to 500 passes as a percent of the damage caused by trampling) plotted against the resistance index (mean relative cover after 0 to 500 passes) for the three main species in the four vegetation types. Resilience (or recovery) of relative cover is similar between stands of *Rubus fruticosus* agg. and *Pteridium aquilinum*, but there is only a marginal increase in resilience two years after trampling in *Pteridium aquilinum*.

The relationship between the resistance index and the tolerance index (mean relative cover one or two years after 0 to 500 passes) for the three major species in the four vegetation types is shown in Fig. 3.11. Primary indices of both *Hyacinthoides non-scripta* stands are below the line of zero resilience (the perpendicular distance from the line of equal resistance and tolerance), and thus negative. Recovery after two years (secondary index) is more favourable, with a high increase in the tolerance index in the *Hyacinthoides non-scripta* (deciduous) stand. *Pteridium aquilinum* has poor resistance, but high resilience and tolerance after one and two seasons of trampling. Finally, *Rubus fruticosus* agg. has low to moderate resistance and moderate to high resilience and tolerance.

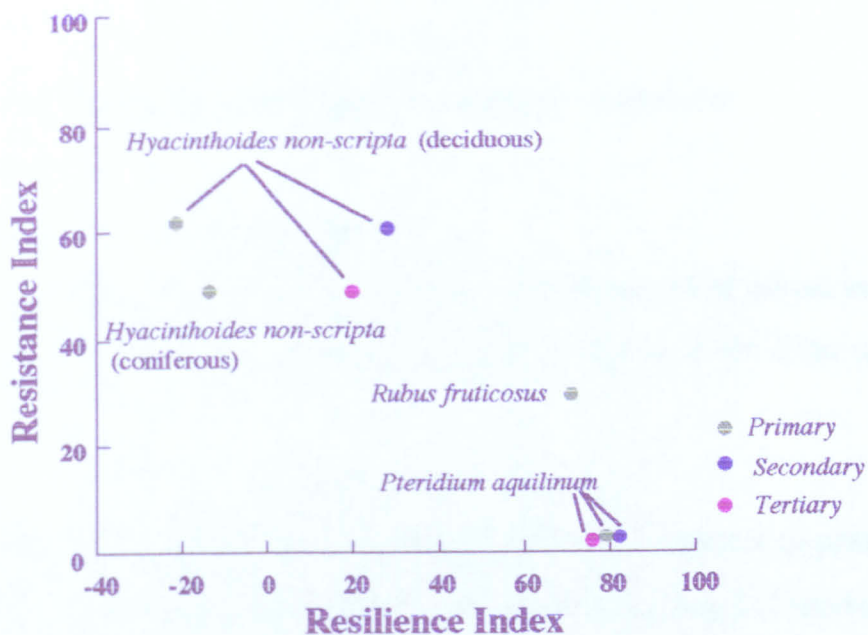


Fig. 3.10 - Indices of resilience and resistance for the four vegetation types, (*Primary* = one seasons trampling and one year of recovery; *Secondary* = one seasons trampling and two years of recovery; *Tertiary* = two seasons trampling and one year of recovery).

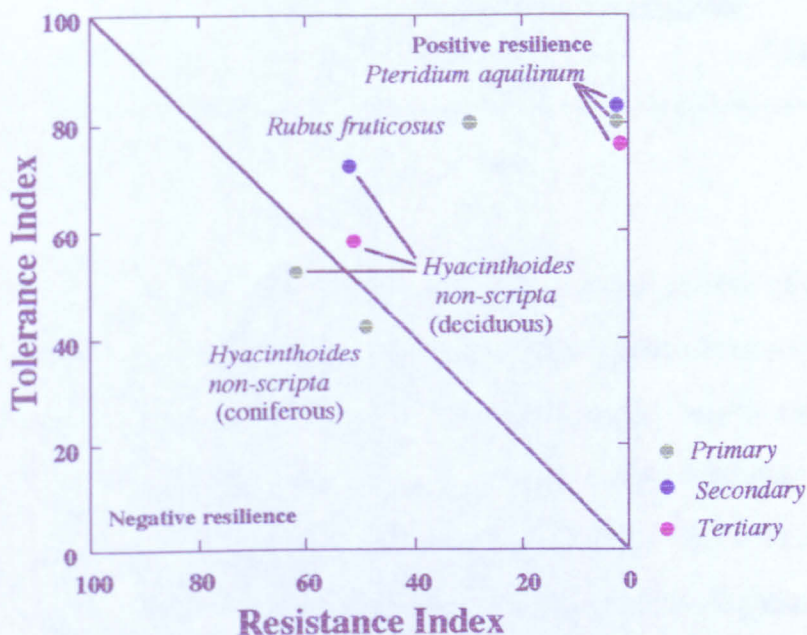


Fig. 3.11 - Resistance, tolerance and resilience of the main species. Resilience is illustrated as the perpendicular distance from the diagonal line of equal resistance and tolerance. (*Primary* = one seasons trampling and one year of recovery; *Secondary* = one seasons trampling and two years of recovery; *Tertiary* = two seasons trampling and one year of recovery).

3.3.10 Long- and short-duration trampling comparisons

3.3.10.1 Vegetation cover

Vegetation cover differs significantly with the number of passes, but responses after and one year after long and short duration trampling do not differ statistically (Table 3.17).

Table 3.17 - Ranked two-way ANOVA and Tukey multiple comparisons for relative cover after trampling and after 1 years recovery for long and short-term trampling in the *Hyacinthoides non-scripta* (deciduous) stand.

Source	After trampling			After 1 year		
	df	F	p	df	F	p
Trampling type	1	0.0	0.986	1	0.9	0.342
Number of passes	4	53.7	>0.0001	4	34.4	>0.0001
Interaction	4	1.4	0.259	4	2.6	0.0541
Significantly Different Treatments^a						
Number of passes	(5,25)≥75>200>500; 25,75)			(5,25,75)>(200,500)		
Trampling type ^b	LT,ST			LT,ST		

^a - significant at $p \leq 0.001$

^b - LT = long-term trampling; ST = short-term trampling

By decreasing with each successive increase in the number of passes, relative cover loss after long-term trampling follows a similar pattern to that outlined for short-term trampling (Fig. 3.12). However, the rate of cover loss is more rapid after long-duration trampling, e.g.: a 50 % cover loss is caused by 250 passes. After the ten week period of 500 passes, relative cover drops to 29 %. This is 14 % lower than remaining cover after short-duration trampling, implying that at heavier levels of trampling, long-term trampling is more damaging. Recovery after one year is negative, with relative cover declining by 13 % after 200 passes.

Polynomial (second-order) regression models best approximate the relationship between long-duration trampling intensity and vegetation cover (Table 3.5).

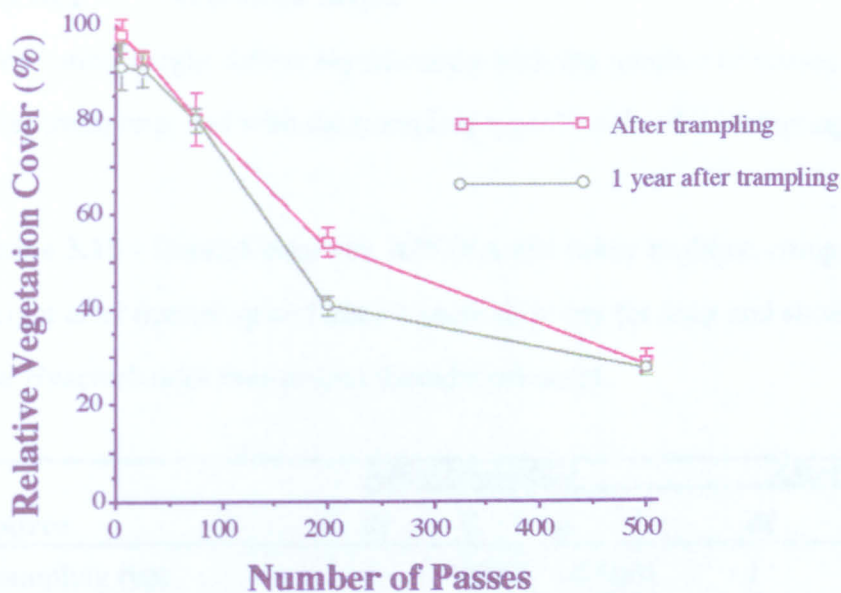


Fig. 3.12 - Relative vegetation cover after long-term trampling spread over ten weeks and after one year of recovery in a *Hyacinthoides non-scripta* (deciduous) sub-community. Vertical bars show one standard error above and below the mean.

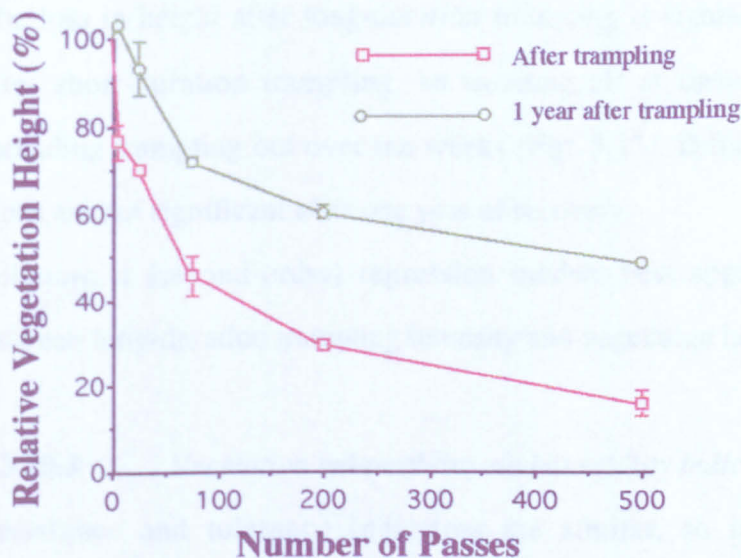


Fig. 3.13 - Relative vegetation height after long-term trampling spread over ten weeks and after one year of recovery in a *Hyacinthoides non-scripta* (deciduous) sub-community. Vertical bars show one standard error above and below the mean.

3.3.10.2 Vegetation height

Vegetation height differs significantly with the number of passes after and one year after trampling, and with the trampling type directly after trampling (Table 3.18).

Table 3.18 - Ranked two-way ANOVA and tukey multiple comparisons for relative height after trampling and after 1 years recovery for long and short-term trampling in the *Hyacinthoides non-scripta* (deciduous) stand.

Source	After trampling			After 1 year		
	df	F	p	df	F	p
Trampling type	1	109.2	>0.0001	1	1.3	0.270
Number of passes	4	62.7	>0.0001	4	37.8	>0.0001
Interaction	4	1.9	0.145	4	0.2	0.945
Significantly Different Treatments^a						
Number of passes	(5>25>75>200>500)			(5,25,75)≥(200,500); 75,200		
Trampling type ^b	LT>ST			LT,ST		

^a - significant at $p \leq 0.001$

^b - LT = long-term trampling; ST = short-term trampling

The loss in height after long-duration trampling is significantly more reduced than after short-duration trampling, so treading all at once is more damaging than spreading trampling out over ten weeks (Fig. 3.13). Differences between trampling types are not significant after one year of recovery.

Polynomial (second-order) regression models best approximate the relationship between long-duration trampling intensity and vegetation height (Table 3.9).

3.3.10.3 Vegetation vulnerability and durability indices

Resistance and tolerance indicators are similar, so irrespective of trampling frequency. For instance, the resistance and tolerance indicators of relative cover are both just 7 % lower than the same index after short-duration trampling. Evident paths are caused by a three weeks of moderate (20 passes per week) and two weeks of heavy (50 passes per week) trampling.

The species specific response of relative cover of *Hyacinthoides non-scripta* (long-term trampling; deciduous) is similar to the entire vegetation type (Table 3.16). Primary resistance and resilience indices based on relative cover are also similar to the vegetation response in the coniferous stand of *Hyacinthoides non-scripta*. Tolerance is low to moderate, resistance is moderate to high and resilience is low.

Chapter 3

PART TWO

**The impact of short-duration experimental trampling on the
flowering and seeding dynamics of deciduous and coniferous
stands of *Hyacinthoides non-scripta***

3.4 Results

The differences in pre-treatment seed and flower characteristics between the coniferous and deciduous *Hyacinthoides non-scripta* stands are startling (Table 3.19). Before trampling, the partially shaded deciduous woodland microclimate affords more favourable conditions for seed and flower production than heavily shaded coniferous stands. For example, the number of flower and seeds produced by stands beneath coniferous cover are up to a quarter of those recorded for stands beneath deciduous cover.

Table 3.19 - Mean control values for the eleven flowering and seeding response variables recorded in pre-treatment lanes for deciduous and coniferous stands of *Hyacinthoides non-scripta*.

<i>Response variable</i>	<i>Vegetation type</i>	
	<i>Deciduous (partial shade)</i>	<i>Coniferous (closed shade)</i>
No. flowering scapes / 0.15m ²	30.5 ± 2.8	17.4 ± 1.2
Scape height (cm)	35.2 ± 0.8	18.1 ± 0.5
No. flowers per scape	8.7 ± 0.7	5.1 ± 0.2
No. flowers / 0.15 cm ²	274 ± 38	88 ± 6
No. seeding scapes / 0.15 cm ²	70.0 ± 4.3	30.0 ± 1.8
Scape height (cm)	38.5 ± 0.6	32.8 ± 0.4
No. capsules / 0.15 cm ²	206 ± 3	82 ± 4
No. capsules per scape	2.9 ± 0.1	2.8 ± 0.3
No. seeds per scape	34.0 ± 0.7	19.9 ± 2.0
No. seeds per capsule	11.6 ± 0.2	7.2 ± 0.1
No. seeds / 0.15 cm ²	2383 ± 64	587 ± 29

3.4.1 Flowering response to short-duration trampling

3.4.1.1 After one season's trampling and one and two years recovery

The response of the four flowering characteristics differs significantly with the trampling intensity after and one year after trampling (Table 3.20). Probabilities are

high (i.e.: typically: $p \leq 0.10$) but non-significant between deciduous and coniferous stands after trampling for most flowering characteristics.

Table 3.20 - Summary of relative response of flowering after trampling and with one years recovery according to the results of Tukey HSD tests for the two *Hyacinthoides non-scripta* stands.

Response variable	After trampling	After 1 year
Flowering scape abundance		
number of passes ^a	5>(25,75)>200>500	(5,25,75)>200>500)
light climate ^b	D,C	D,C
Flowering scape height		
number of passes	5>(25,75)>200>500	(5>25>75>200>500)
light climate	D,C	D,C
Number of flowers per scape		
number of passes	5>(25,75)≥200>500; 75,200	(5,25)>(75,200)>500
light climate	D,C	D,C
Number of flowers		
number of passes	(5>25>75>200>500)	(5,25)>75>200>500
light climate	D,C	D,C

^a - significant at $p \leq 0.001$

^b - D = deciduous (0.7 of full daylight); C = coniferous (0.3 of full daylight); all non-significant

In both stands, all flowering response variables decline rapidly with trampling intensity. This trend is illustrated for flowering scape abundance (Fig. 3.14) and the number of flowers (Fig. 3.15). 500 passes in the deciduous stand reduces the number of flowers to just 4 % of control vegetation, and eradicates flower production completely in the coniferous stand. Between 75 and 120 passes causes a 50 % loss in both stands.

Recovery of flowering response variables are generally negative one year after trampling. The number of flowers per scape undergoes the poorest recovery by declining by 19 % and 11 % after 200 passes in the coniferous and deciduous stands respectively. After two years of recovery, the responses of scape height and the number of flowers are more encouraging in the deciduous stand, but values for the

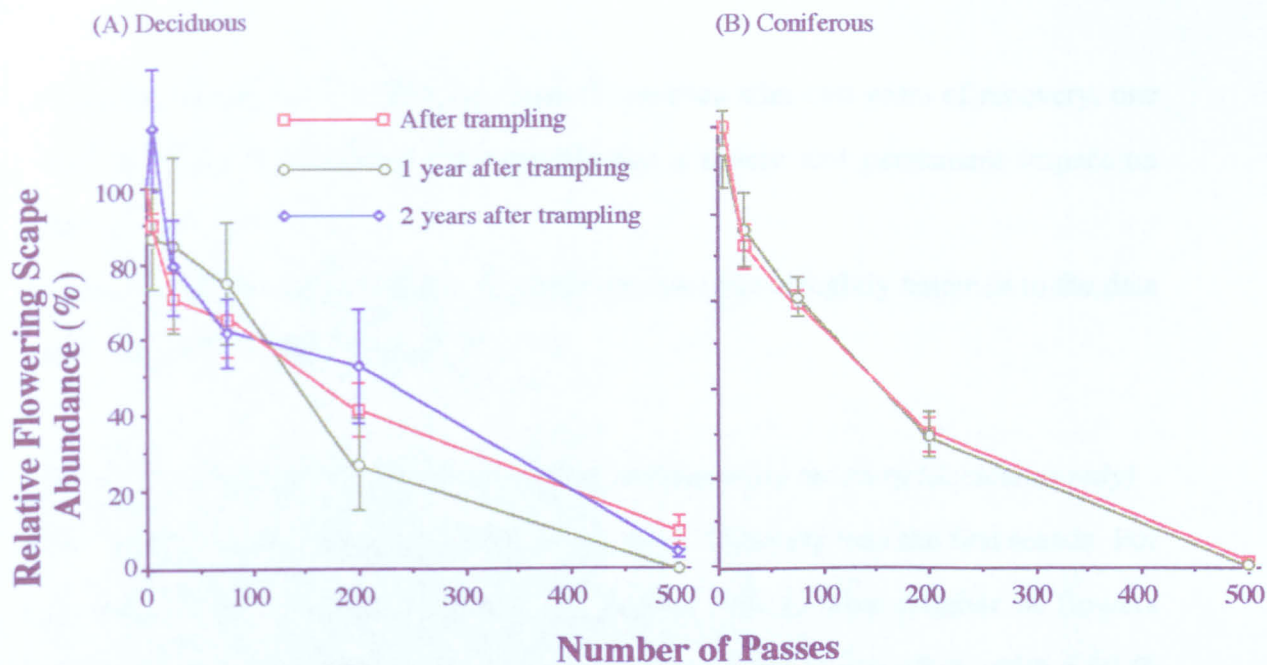


Fig. 3.14 - Relative flowering scape abundance after trampling and after one and two (A) only) years of recovery in deciduous and coniferous stands of *Hyacinthoides non-scripta*. Vertical bars depict one standard error above and below the mean.

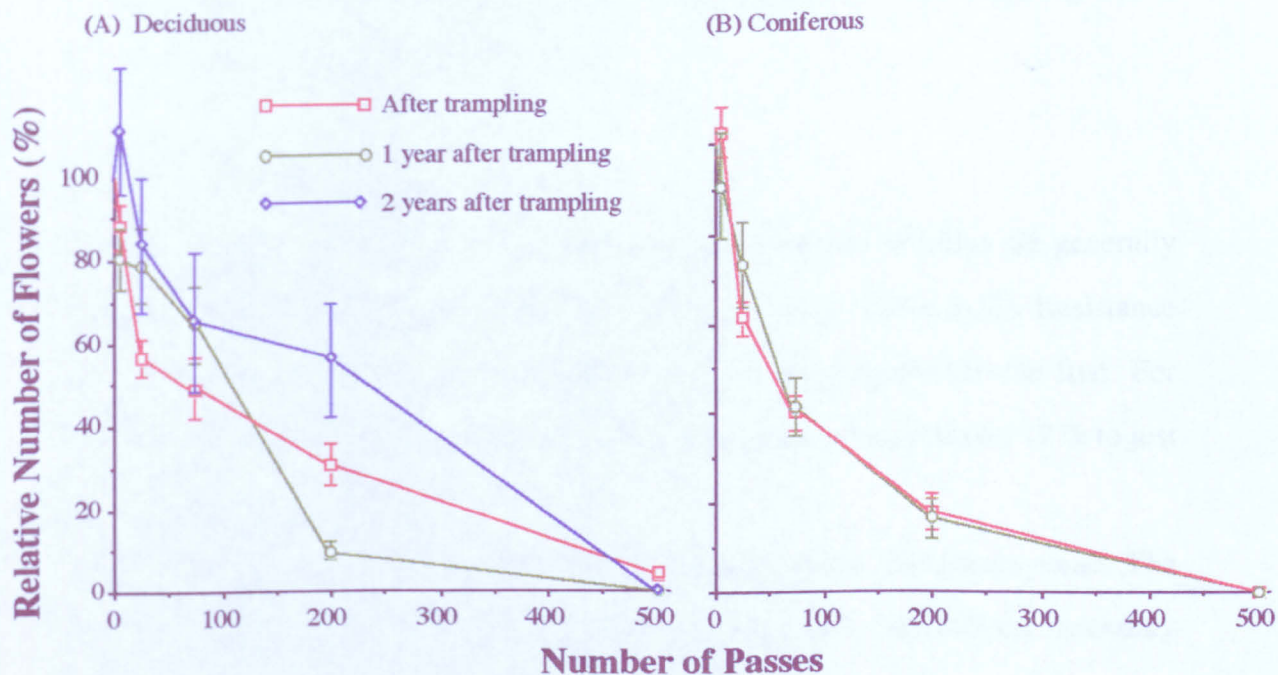


Fig. 3.15 - Relative number of flowers after trampling and after one and two (A) only) years of recovery in deciduous and coniferous stands of *Hyacinthoides non-scripta*. Vertical bars depict one standard error above and below the mean.

latter are still zero in the 500 pass lanes. Thus, even after two years of recovery, one season of heavy trampling (500 passes) has a severe and permanent impact on flowering.

The polynomial (second-order) regression models offer a slightly better fit to the data than the linear models (Table 3.21).

3.4.1.2 *After two seasons' trampling and one years recovery (deciduous only)*

The impact of a second seasons' trampling is more damaging than the first season. For example, after a second increment of 75 passes the relative number of flowers declines by 34 % from the response after a first season to just 15 %, with a 50 % relative loss occurring after 30 passes. Recovery after one year is slight but positive for all flowering response variables.

The trend of the best approximation of the relationship between trampling intensity and flowering response being given by the polynomial (second-order) regression models is again confirmed (Table 3.21).

3.4.1.3 *Flowering vulnerability*

Primary resistance indices generated for flowering response variables are generally higher in deciduous stands compared to coniferous stands (Table 3.22). Resistance declines in all response variables after a second season compared to the first. For example, the relative number of flowers in deciduous stands plummets by 17 % to just 13 % after a second season.

After one year, recovery is slightly more favourable in the coniferous stand. The number of flowers per scape shows the poorest primary resilience, and the secondary resilience index is still negative after two years of recovery.

Table 3.21 - Polynomial (second-order) regression models that approximate the relationship between short-duration trampling intensity (0 to 500 passes) and relative flowering response after, 1 and 2 years after, after a second season and a subsequent year after for the two *Hyacinthoides non-scripta* stands. Linear regression coefficients of determination (r^2) are also provided.

<i>Response variable</i>	<i>Regression model</i>	<i>Polynomial r^2</i>	<i>Linear r^2</i>
Flowering scape number			
<i>Deciduous</i>			
After 1st	$Y = 90.1 - 0.33x + 0.00035x^2$	0.953	0.893
1 year after	$Y = 96.1 - 0.41x + 0.00044x^2$	0.982	0.866
2 years after	$Y = 99.2 - 0.34x + 0.00029x^2$	0.906	0.874
After 2nd	$Y = 85.2 - 0.58x + 0.00083x^2$	0.867	0.635
1 year after	$Y = 106.2 - 0.56x + 0.00070x^2$	0.948	0.812
<i>Coniferous</i>			
After 1st	$Y = 94.9 - 0.45x + 0.00053x^2$	0.969	0.864
1 year after	$Y = 94.4 - 0.44x + 0.00051x^2$	0.985	0.888
Scape height			
<i>Deciduous</i>			
After 1st	$Y = 94.2 - 0.32x + 0.00035x^2$	0.982	0.905
1 year after	$Y = 103.1 - 0.27x + 0.00012x^2$	0.996	0.991
2 years after	$Y = 89.3 - 0.14x + 0.00003x^2$	0.904	0.903
After 2nd	$Y = 90.5 - 0.38x + 0.00040x^2$	0.933	0.867
1 year after	$Y = 101.7 - 0.29x + 0.00018x^2$	0.995	0.983
<i>Coniferous</i>			
After 1st	$Y = 97.6 - 0.26x + 0.00015x^2$	0.996	0.986
1 year after	$Y = 98.4 - 0.22x + 0.00005x^2$	0.999	0.998
No. flowers / scape			
<i>Deciduous</i>			
After 1st	$Y = 94.3 - 0.13x + 0.00002x^2$	0.923	0.922
1 year after ^a	$Y = 11846.0 - 39.7x + 0.031x^2$	0.909	0.886
2 years after ^a	$Y = 9505.3 - 12.9x + 0.012x^2$	0.940	0.931
After 2nd	$Y = 88.3 - 0.28x + 0.00020x^2$	0.962	0.944
1 year after	$Y = 101.1 - 0.21x + 0.00002x^2$	0.979	0.978
<i>Coniferous</i>			
After 1st	$Y = 96.7 - 0.24x + 0.00010x^2$	0.961	0.957
1 year after	$Y = 98.2 - 0.38x + 0.00037x^2$	0.992	0.941
Flower abundance			
<i>Deciduous</i>			
After 1st	$Y = 85.2 - 0.41x + 0.0005x^2$	0.886	0.771
1 year after	$Y = 93.5 - 0.54x + 0.0007x^2$	0.801	0.801
2 years after	$Y = 106.7 - 0.37x + 0.0003x^2$	0.867	0.839
After 2nd	$Y = 76.9 - 0.59x + 0.0009x^2$	0.825	0.550
1 year after	$Y = 116.9 - 0.67x + 0.0009x^2$	0.878	0.725
<i>Coniferous</i>			
After 1st	$Y = 92.0 - 0.58x + 0.0008x^2$	0.911	0.709
1 year after	$Y = 91.6 - 0.57x + 0.0008x^2$	0.964	0.759

^a - ($X = X^2$) transformed

Table 3.22 - Flowering response in terms of resistance, resilience and tolerance to one or two seasons short-duration trampling in the two stand types of *Hyacinthoides non-scripta*.

Index	Light climate / Durability indices ^a			
	Deciduous			Coniferous
	Pri	Sec	Ter	Pri
Resistance indicators ^b				
Relative number of flowering scapes (%)	39	—	18	31
Relative flowering scape height (%)	46	—	33	47
Relative number of flowers per scape (%)	64	—	39	46
Relative number of flowers (%)	30	—	13	18
Resilience indicators ^c				
Relative number of flowering scapes (%)	-11	6	14	1
Relative flowering scape height (%)	2	18	18	3
Relative number of flowers per scape (%)	-27	-13	15	-15
Relative number of flowers (%)	-9	21	19	1
Tolerance indicators ^d				
Relative number of flowering scapes (%)	33	43	30	31
Relative flowering scape height (%)	47	56	45	48
Relative number of flowers per scape (%)	54	59	48	38
Relative number of flowers (%)	24	45	29	18

^a - Pri = primary durability index based on one year recovery; Sec = secondary durability index based on two years recovery; Ter = tertiary durability index based on one years recovery from the second season.

^b - mean relative 'variable' after 0 to 500 passes

^c - mean increase in relative 'variable' 1 or 2 years after 0 to 500 passes, as a percent of the damage caused by trampling

^d - mean relative 'variable' 1 or 2 year after 0 to 500 passes

Tolerance of flowering response variables in the deciduous stand is generally greater than the coniferous stand. Again, number of flowers per scape has the highest primary tolerance and number of flowers the lowest. Secondary tolerance indices for the flowering response variables all increase when compared to the primary indices, with the tertiary tolerance indices one year after a second seasons trampling very similar on all counts to the primary tolerance indices.

3.4.2 Trampling impact on the seeding ability

3.4.2.1 After one season's trampling and one and two years recovery

The response of all seven relative seed characteristics differs significantly with the number of passes after and one year after trampling (Table 3.23). Seeding scape abundance and capsule abundance differ significantly with light climate after trampling, as does the number of seeds per scape one year after trampling. The number of seeds per capsule and overall seed abundance differ significantly with light climate after *and* one year after trampling. In all cases, the rate of loss is highest in the heavily shaded coniferous stand. Differences one year after trampling are lower in magnitude than after trampling for seeding scape abundance, scape abundance and seed abundance but higher in magnitude for seeds per capsule and seeds per scape.

In both ^{ground flora types} ~~sub-communities~~, all seeding response variables rapidly decrease with each successive increase in the number of passes. This is illustrated for seeding scape abundance (Fig. 3.16) and number of seeds (Fig. 3.17). One season of heavy trampling (500 passes) is sufficient to completely eradicate the ability to produce seed-bearing structures in the coniferous stand. In the deciduous stand, heavy trampling eradicates most seeding response variables with the exception of relative scape number and height, which decline to 10 % and 24 % respectively. The most sensitive variable in both stands is the relative number of seeds, where a 50 % loss is caused by 50 and 25 passes in the deciduous and coniferous stands respectively.

Response after a year's ¹ recovery is either negative or poor for all seeding response variables in both sub-communities. Although the rate of recovery of scape height is poor, the response up to 200 passes enables plants to recover scape height to 89 % of the control vegetation. One year after 200 passes, the number of seeds is just 1 % and 5 % of control vegetation in the deciduous and coniferous stands respectively. Even after a second year of recovery, plants are still unable to induce seeding characteristics from trampling thresholds of 500 passes.

Table 3.23 - Summary of relative response of seeding after trampling and with one years recovery according to the results of Tukey HSD tests for the two *Hyacinthoides non-scripta* stands.

Response variable	<i>After trampling</i>	<i>After 1 year</i>
Seeding scape abundance		
number of passes ^a	5>(25,75)>200>500	5>(25,75)>200>500)
light climate ^b	D>C	D,C
Seeding scape height		
number of passes	(5,25)>75>200>500	(5,25,75)≥(200,500); 25,75,200
light climate	D,C	D,C
Capsule abundance		
number of passes	(5>25>75>200>500)	(5>25>75>200>500)
light climate	D>C	D,C
Number of capsules per scape		
number of passes	(5,25,75)≥(200,500); 75,200	(5,25,75)≥(200,500); 25,200
light climate	D,C	D,C
Number of seeds per scape		
number of passes	5>(25,75)>200>500	5>(25,75)>200>500
light climate	D,C	D>C
Number of seeds per capsule		
number of passes	5>25>75>200>500	5>(25,75)>200>500
light climate	D>C	D>C
Seed abundance		
number of passes	(5>25>75>200>500)	5>(25,75)>200>500
light climate	D>C	D>C

^a - significant at $p \leq 0.001$

^b - D = deciduous (0.7 of full daylight); C = coniferous (0.3 of full daylight); where significant, $p \leq 0.05$

Once again, the polynomial (second-order) regression models fit the data marginally better than the linear models (Table 3.24).

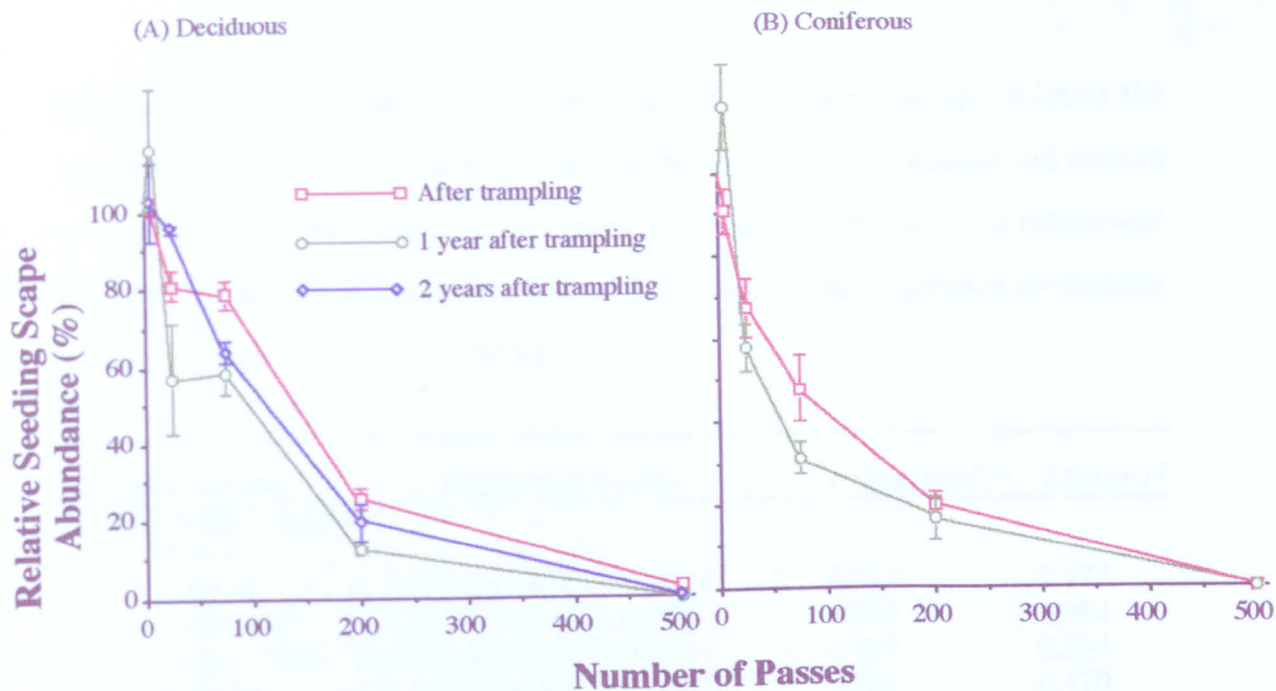


Fig. 3.16 - Relative seeding scape abundance after trampling and after one and two (A) only) years of recovery in deciduous and coniferous stands of *Hyacinthoides non-scripta*. Vertical bars depict one standard error above and below the mean.

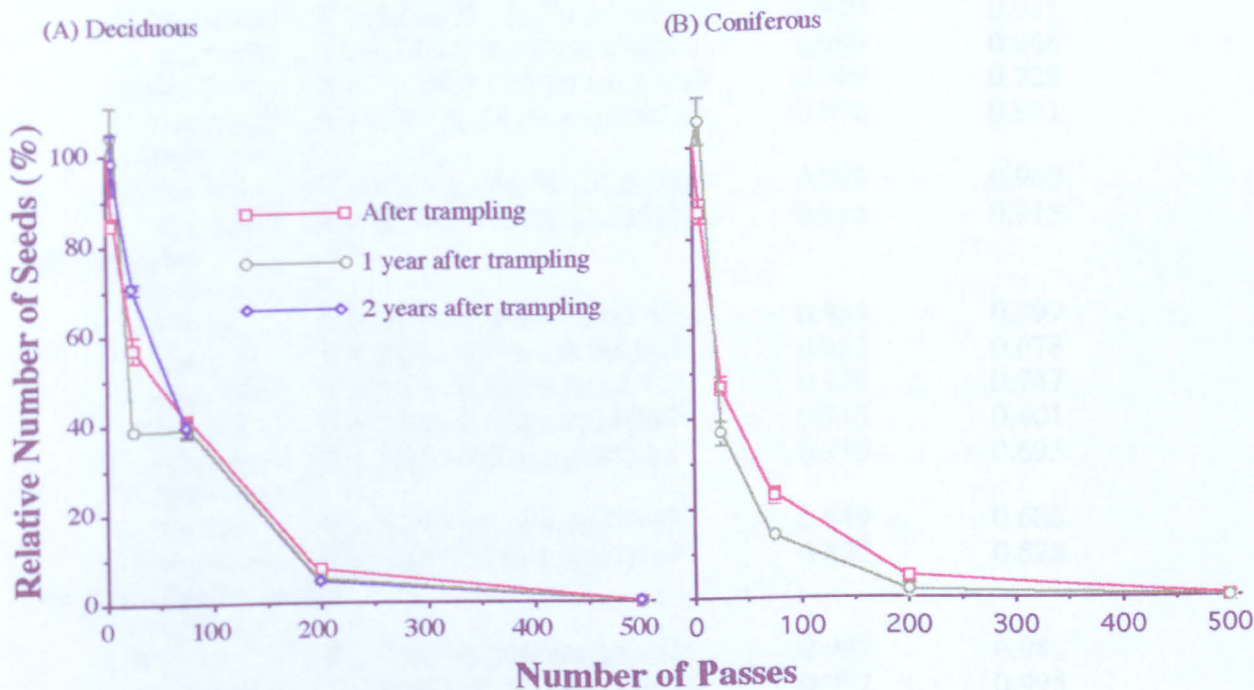


Fig. 3.17 - Relative number of seeds after trampling and after one and two (A) only) years of recovery in deciduous and coniferous stands of *Hyacinthoides non-scripta*. Vertical bars depict one standard error above and below the mean.

Table 3.24 - Polynomial (second-order) regression models that approximate the relationship between short-duration trampling intensity (0 to 500 passes) and relative seeding response after, 1 and 2 years after, after a second season and a subsequent year after for the two *Hyacinthoides non-scripta* stands. Linear regression coefficients of determination (r^2) are also provided.

<i>Response variable</i>	<i>Regression model</i>	<i>Polynomial r^2</i>	<i>Linear r^2</i>
Seeding scape number			
<i>Deciduous</i>			
After 1st	$Y = 101.1 - 0.47x + 0.0005x^2$	0.977	0.878
1 year after	$Y = 98.8 - 0.62x + 0.0009x^2$	0.889	0.694
2 years after	$Y = 104.4 - 0.57x + 0.0007x^2$	0.995	0.844
After 2nd	$Y = 70.5 - 0.60x + 0.0009x^2$	0.786	0.470
1 year after	$Y = 112.4 - 0.70x + 0.0009x^2$	0.975	0.771
<i>Coniferous</i>			
After 1st	$Y = 90.4 - 0.52x + 0.0007x^2$	0.962	0.793
1 year after	$Y = 98.4 - 0.68x + 0.0010x^2$	0.816	0.593
Scape height			
<i>Deciduous</i>			
After 1st	$Y = 97.8 - 0.22x + 0.0003x^2$	0.977	0.713
1 year after ^a	$Y = 10121.7 - 11.7x + 0.017x^2$	0.940	0.931
2 years after	$Y = 93.6 - 0.071x + 0.0002x^2$	0.989	0.966
After 2nd ^a	$Y = 12068.2 - 75.3x + 0.102x^2$	0.918	0.728
1 year after ^a	$Y = 8095.5 - 14.0x + 0.0041x^2$	0.892	0.891
<i>Coniferous</i>			
After 1st ^a	$Y = 9019.1 - 18.3x + 0.0008x^2$	0.969	0.969
1 year after ^a	$Y = 8576.5 - 15.2x + 0.0035x^2$	0.915	0.915
No. capsules			
<i>Deciduous</i>			
After 1st	$Y = 92.5 - 0.55x + 0.0007x^2$	0.984	0.799
1 year after	$Y = 93.8 - 0.65x + 0.0009x^2$	0.927	0.678
2 years after	$Y = 96.7 - 0.63x + 0.0009x^2$	0.976	0.747
After 2nd	$Y = 70.0 - 0.63x + 0.0010x^2$	0.713	0.401
1 year after	$Y = 86.1 - 0.60x + 0.0009x^2$	0.959	0.695
<i>Coniferous</i>			
After 1st	$Y = 87.9 - 0.61x + 0.0009x^2$	0.949	0.688
1 year after	$Y = 94.7 - 0.76x + 0.0011x^2$	0.827	0.528
No. capsules per scape			
<i>Deciduous</i>			
After 1st	$Y = 93.2 - 0.24x + 0.0001x^2$	0.987	0.981
1 year after	$Y = 100.7 - 0.23x + 0.0001x^2$	0.997	0.995
2 years after	$Y = 92.5 - 0.14x - 0.0001x^2$	0.944	0.940
After 2nd	$Y = 97.4 - 0.68x + 0.0010x^2$	0.930	0.677
1 year after	$Y = 80.5 - 0.19x + 0.0001x^2$	0.881	0.879
<i>Coniferous</i>			
After 1st	$Y = 98.2 - 0.30x + 0.0002x^2$	0.999	0.982
1 year after	$Y = 99.6 - 0.31x + 0.0002x^2$	0.997	0.977

<i>Response variable</i>	<i>Regression model</i>	<i>Polynomial r²</i>	<i>Linear r²</i>
No. seeds per pod			
<i>Deciduous</i>			
After 1st	$Y = 93.7 - 0.22x + 0.0001x^2$	0.976	0.974
1 year after	$Y = 90.5 - 0.053x - 0.0003x^2$	0.968	0.939
2 years after	$Y = 98.0 - 0.12x - 0.0002x^2$	0.994	0.984
After 2nd	$Y = 104.8 - 0.66x + 0.0009x^2$	0.963	0.760
1 year after	$Y = 94.8 - 0.16x + 0.0001x^2$	0.960	0.959
<i>Coniferous</i>			
After 1st	$Y = 92.4 - 0.24x + 0.0001x^2$	0.939	0.933
1 year after	$Y = 88.6 - 0.24x + 0.0001x^2$	0.945	0.938
No. seeds per scape			
<i>Deciduous</i>			
After 1st	$Y = 91.5 - 0.35x + 0.0003x^2$	0.926	0.882
1 year after	$Y = 92.2 - 0.32x + 0.0003x^2$	0.968	0.937
2 years after	$Y = 91.7 - 0.30x + 0.0002x^2$	0.950	0.926
After 2nd	$Y = 100.1 - 0.77x + 0.0011x^2$	0.840	0.563
1 year after	$Y = 76.2 - 0.33x + 0.0004x^2$	0.830	0.766
<i>Coniferous</i>			
After 1st	$Y = 93.7 - 0.50x + 0.0006x^2$	0.974	0.832
1 year after	$Y = 88.5 - 0.47x + 0.0006x^2$	0.942	0.803
Seed abundance			
<i>Deciduous</i>			
After 1st	$Y = 86.2 - 0.59x + 0.0008x^2$	0.940	0.690
1 year after	$Y = 87.9 - 0.65x + 0.0009x^2$	0.828	0.573
2 years after	$Y = 94.8 - 0.68x + 0.0010x^2$	0.972	0.689
After 2nd	$Y = 67.1 - 0.61x + 0.0010x^2$	0.685	0.378
1 year after	$Y = 72.4 - 0.55x + 0.0008x^2$	0.826	0.555
<i>Coniferous</i>			
After 1st	$Y = 82.0 - 0.64x + 0.0010x^2$	0.867	0.569
1 year after	$Y = 85.5 - 0.73x + 0.0011x^2$	0.779	0.463

^a - ($X = X^2$) transformed

3.4.2.2 *After two seasons trampling and one years recovery*

The seed variables all differ significantly with the number of passes after a further seasons trampling, and with the subsequent year of recovery. A second season of heavy trampling (500 passes) has a devastating effect on seeding dynamics. For instance, seed scape abundance is reduced to 13 % of controls after two seasons of 75 passes, and no seed bearing structures are produced after a second season of 200 passes at all. A 50 % relative loss in the number of seeds occurs at 15 passes.

Relationships between number of passes and seeding response are best approximated by using polynomial (second-order) regression models (Table 3.24).

3.4.2.3 *Seeding vulnerability*

Primary resistance indices are higher in the deciduous stand compared to the coniferous stand for seeding scape abundance, scape height, number of capsules and number of seeds (Table 3.25).

Table 3.25 - Seeding response in terms of resistance, resilience and tolerance to one or two seasons short-duration trampling in the two stand types of *Hyacinthoides non-scripta*.

Index	Light climate / Durability indices^a			
	Deciduous		Coniferous	
	<i>Pri</i>	<i>Sec</i>	<i>Ter</i>	<i>Pri</i>
Resistance indicators^b				
Relative number of seeding scapes (%)	34	—	8	25
Relative seeding scape height (%)	73	—	27	57
Relative number of capsules (%)	23	—	6	18
Relative number of capsules per scape (%)	43	—	17	45
Relative number of seeds per capsule (%)	46	—	23	44
Relative number of seeds per scape (%)	25	—	15	28
Relative number of seeds (%)	16	—	5	12
Resilience indicators^c				
Relative number of seeding scapes (%)	-18	-6	18	-7
Relative seeding scape height (%)	-35	-39	37	1
Relative number of capsules (%)	-7	2	11	-7
Relative number of capsules per scape (%)	7	7	26	-3
Relative number of seeds per capsule (%)	16	14	33	-4
Relative number of seeds per scape (%)	12	19	16	-3
Relative number of seeds (%)	-1	1	6	-4
Tolerance indicators^d				
Relative number of seeding scapes (%)	22	30	24	20
Relative seeding scape height (%)	63	54	54	57
Relative number of capsules (%)	17	21	16	12
Relative number of capsules per scape (%)	47	47	39	43
Relative number of seeds per capsule (%)	55	54	48	41
Relative number of seeds per scape (%)	33	39	28	26
Relative number of seeds (%)	15	17	10	8

^a - *Pri* = primary durability index based on one year recovery; *Sec* = secondary durability index based on two years recovery; *Ter* = tertiary durability index based on one years recovery from the second season.

^b - mean relative 'variable' after 0 to 500 passes

^c - mean increase in relative 'variable' 1 or 2 years after 0 to 500 passes, as a percent of the damage caused by trampling

^d - mean relative 'variable' 1 or 2 year after 0 to 500 passes

A second season of trampling has a devastating and cumulative impact on seeding characteristics, with the secondary resistance indices all lower than the primary indices. The secondary resistance index of the number of seeds falls to 5 % of the control, and the biggest drop between primary and secondary indices occurs in scape

height. The worst primary resilience occurs in the deciduous stand for scape abundance and scape height, which both continue to decline after two years of recovery.

Primary tolerance indices are either similar or marginally greater in deciduous stands compared to coniferous stands. The primary tolerance index is highest for capsules per scape, scape height and seeds per capsule in both stand types. Generally, the marginally higher values for the secondary tolerance index indicate that a second year benefits recovery. The tertiary tolerance indices for seeding characteristics are marginally lower one year after a second seasons trampling than the primary tolerance indices.

3.4.3 Conclusion

In summary, the ^{major}~~greatest~~ impact ^{is}~~occurs~~ on the ability of the plant to produce seed, and it is apparent that seed characteristics are more vulnerable to trampling than flower characteristics. Both are more sensitive to trampling than all other physiognomic parameters.

Chapter 4

THE RESISTANCE AND RECOVERY OF WOODLAND GROUND FLORA AND FOOTPATH SPECIES TO SIMULATED TRAMPLING

4.1 Introduction

This chapter presents a set of investigations that attempt to separate the qualities of plants to resist wear from those that contribute to survival and recovery after damage. Using a simulated trampling method, the subsequent quantification of the ability of species to resist and recover from various intensities of trampling provides an integral basis for their management in woodland sites.

4.1.1 *Research proposals*

- To augment the autecological accounts of woodland and footpath species selected for study by examining their response to light and heavy levels of trampling.
- To advance the understanding of the relationship between resistance to and recovery from trampling for species in shaded and open microclimates.
- To define an arbitrary classification system of plant strategies exhibited by plant species that are tolerant of trampling.
- To quantify plant growth strategies, morphological adaptations and physiological responses of vegetation tolerant of trampling so that land managers can evaluate the potential of vegetated sites to withstand recreational use.
- To identify vulnerable species to aid with habitat zoning and recreation management, and to provide a measure of the potential of species to survive, invade, regenerate and revegetate eroded areas in woodlands.

4.2 Materials and Methods

^{like} Methodology was adapted from the procedures of Kellomaki (1973), Kellomaki & Saastamowen (1975), Sun & Liddle (1991) and Sun (1992).

4.2.1 Species studied and experimental blocks

A total of sixteen species were studied in four discrete experimental blocks:

- i). **block one** - 15th April 1995 to 21st August 1995; *Mercurialis perennis*, *Poa pratensis*, *Holcus lanatus*, *Deschampsia cespitosa*, *D. flexuosa*, *Plantago lanceolata*.
- ii). **block two** - October 2nd 1995 to February 6th 1996; *Lolium perenne*, *Taraxacum officinale*, *Teucrium scorodonia*, *Brachypodium sylvaticum*.
- iii). **block three** - February 15th 1996 to June 23rd 1996; *Ranunculus ficaria*, *Oxalis acetosella*, *Anemone nemorosa*, *Plantago major*, *Silene dioica*, *Geum urbanum*.
- iv). **block four** - ran in tandem with block three; *Plantago major*, *Silene dioica*, *Geum urbanum*.

Blocks one, two and three quantified the response of selected species to simulated trampling in open microclimates, whilst block four examined the additional stress of shade on treated plants.

The selection of species satisfied the following criteria:

- species were present in the woodlands surveyed in Chapter 2
- selection was representative of a range of growth and life-form strategies
- seeds or ^{planted} ~~transported~~ seedlings were obtained directly from local vegetation communities or seed suppliers
- species were representative of trampled rides and footpaths and also of undisturbed areas

Species were successfully germinated, with the exception of *Mercurialis perennis*, *Ranunculus ficaria*, *Oxalis acetosella* and *Anemone nemorosa*, which were transplanted as seedlings directly from local woodlands and hedgerows. Germination

conditions followed criteria expressed for individual species by Grime *et al.* (1988). Species selected for study that ^{failed to germinate} included *Primula vulgaris*, *Viola riviniana* and *Urtica dioica* ~~failed to germinate~~, so were not included.

Germinules and transplanted seedlings were potted up in 20 cm diameter pots filled with a firmed mixture of 75 % local garden soil and 25 % John Innes potting compost. All species were sown at densities of three seedlings per pot, and the soil was kept at two-thirds water capacity by weighing and then watering to a known standard weight. Pots in all the blocks were placed in a glasshouse where the day length was representative of the external environment. Initial germination trials allowed species-specific germination times to be quantified, with seeds sown at different dates in order to synchronise plant age. In addition, the pots of block four were placed beneath a double layer of 2 mm garden mesh, which reduced light levels to approximately 25 % of full daylight and simulated microclimatic conditions caste by a heavily shaded overstorey. Sun & Liddle (1993c) suggested that the differences between species based on their response to light trampling were prone to error and may be misleading. Therefore, only heavy levels of trampling were applied to species for the shade experiment on the plants of block four.

4.2.2 Tamp treatments

The dropped tamp simulated trampling method was based on Sun & Liddle's (1991) interpretation of a method originally outlined by Wagar (1967), and subsequently modified by Kellomaki (1973) and Kellomaki & Saastamowen (1975). A 0.71 kg tamp consisting of a lead weighted round wooden disc of 18 cm diameter was dropped on plants from a falling distance of 0.5 m. By utilising Newton's Second Law of Motion, the velocity of the falling tamp was calculated and used to define the total kinetic energy impulse per unit area. The energy impulse of 0.014 J cm^{-2} generated by the falling tamp was assumed by Kellomaki (1973) and Kellomaki & Saastamowen (1975) to be similar to the force that reaches the ground in normal recreational trampling.

Three different intensities of trampling were used in this study. They were:

0 drops (control)

10 drops (light trampling)

30 drops (heavy trampling)

The simulated trampling treatments commenced seven weeks after germination and five light and heavy simulated trampling treatments were applied at separate seven day intervals in each experimental block.

4.2.3 *Experimental design and recording*

4.2.3.1 *Morphological parameters*

In all four experimental blocks, there were twelve replicate pots in each of the three simulated trampling treatments per species. This gave 72 pots for each of the three trampling treatments in both blocks one and three, 48 pots in block two and 36 pots in block four. To minimise potential positional effects, the position of each pot was randomised each week over the duration of the experiment.

Measurements of plant height (cm), the number of living leaves per plant, mean leaf length (cm), mean leaf width (cm) and the number of living tillers (graminoids only) were obtained for each species before each of the five trampling treatments.

4.2.3.2 *Biomass harvests*

As plant biomass is a comprehensive measure of plant growth, the indication of plant resistance to simulated light and heavy trampling is based on their biomass values (Sun & Liddle 1993b). Biomass harvests were made two days after the final fifth trampling treatments for each species in each sampling block, and then at three two week intervals until the final biomass harvest was obtained 128 days after germination. For each species, plants were cut off at ground level from three pots per treatment type for the purpose of measuring above-ground biomass. Any dead material present as a result of trampling damage was separated from the live parts and

discarded. The above-ground biomass was placed in an oven at 105 °C for 36 hours in order to measure the biomass as 'g per individual plant'. The below-ground roots were also extracted from pots by careful washing and sieving, and below-ground biomass was determined in the same way.

4.2.4 Data analysis

Relative percent values of lightly or heavily trampled morphological parameters were calculated as a percent proportion of the control plants before the final trampling treatment. Relative biomass was calculated as the mean above- or below-ground biomass (g per individual) of lightly or heavily trampled species expressed as a percentage of the control plant biomass (g per individual). This '*resistance index*' was equivalent to the relative above-ground biomass two days after the final simulated trampling treatment (after Sun 1992).

This study generates three linear regression models, with time (weeks) as the independent variable and control, lightly trampled and heavily trampled plant biomass as dependent variables. The '*relative growth rate*' is equivalent to the slope of the linear regression of above-ground control plant biomass at each of the four biomass harvests versus time (weeks) (after Evans 1972). The '*relative recovery rates*' are equal to the slopes of the linear regression of above-ground biomass of lightly and heavily trampled plants at each of the four biomass harvests versus time (weeks). Both relative growth rates and relative recovery rates are expressed as 'g g⁻¹ week⁻¹'.

4.2.5 Statistical analysis

Data sets were analysed using SYSTAT 5.2.1.

4.3 Results

Oxalis acetosella and *Anemone nemorosa* were eradicated between the second and third week of light and heavy trampling. These two species are subsequently absent from further analysis, but all other species survived the simulated trampling treatments. As the four sampling blocks were carried out at different times of the year statistical interpretation of the combined data sets should be dealt with caution, although it is possible to comment upon general observable trends.

4.3.1 Morphological parameters

4.3.1.1 Plant height

Control plant height increases over the experimental period for species (Fig. 4.1a & 4.3a). At the end of the experiment, the tallest species are *Mercurialis perennis*, *Deschampsia cespitosa* and *Lolium perenne* and the shortest are *Silene dioica* and *Ranunculus ficaria*.

Height is reduced by heavy trampling (Fig. 4.2a & Fig. 4.4a), and at the end of the experiment, the relative height of heavily and lightly trampled species is 38 % and 54 % of control plants respectively. Both light and heavy relative heights vary amongst species (Table 4.1).

After heavy trampling, *Poa pratensis*, *Plantago major* and *P. lanceolata* possess the highest relative plant heights, *Mercurialis perennis*, *Teucrium scorodonia*, *Silene dioica* and *Geum urbanum* have the lowest, with remaining species possessing moderate values. Height reduction trends are similar between light and heavy trampling, but *Geum urbanum* has a high relative height after light trampling and *Silene dioica* and *Mercurialis perennis* are the only species with low relative heights.

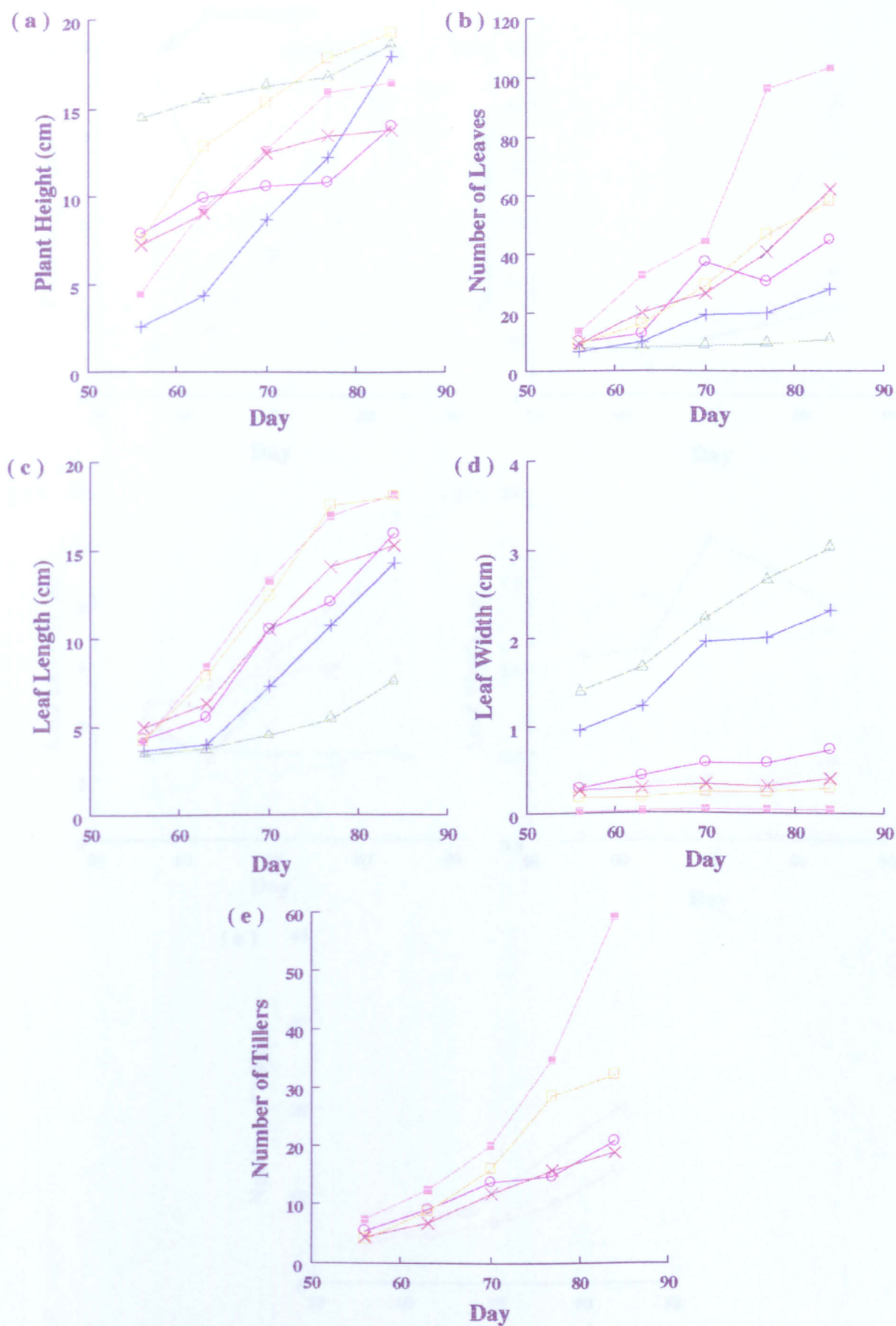


Fig. 4.1 - Growth of morphological parameters over the treatment period for control plants of block one (*Plantago lanceolata*; *Deschampsia flexuosa*; *Poa pratensis*; *Holcus lanatus*; *Deschampsia cespitosa* & *Mercurialis perennis*).

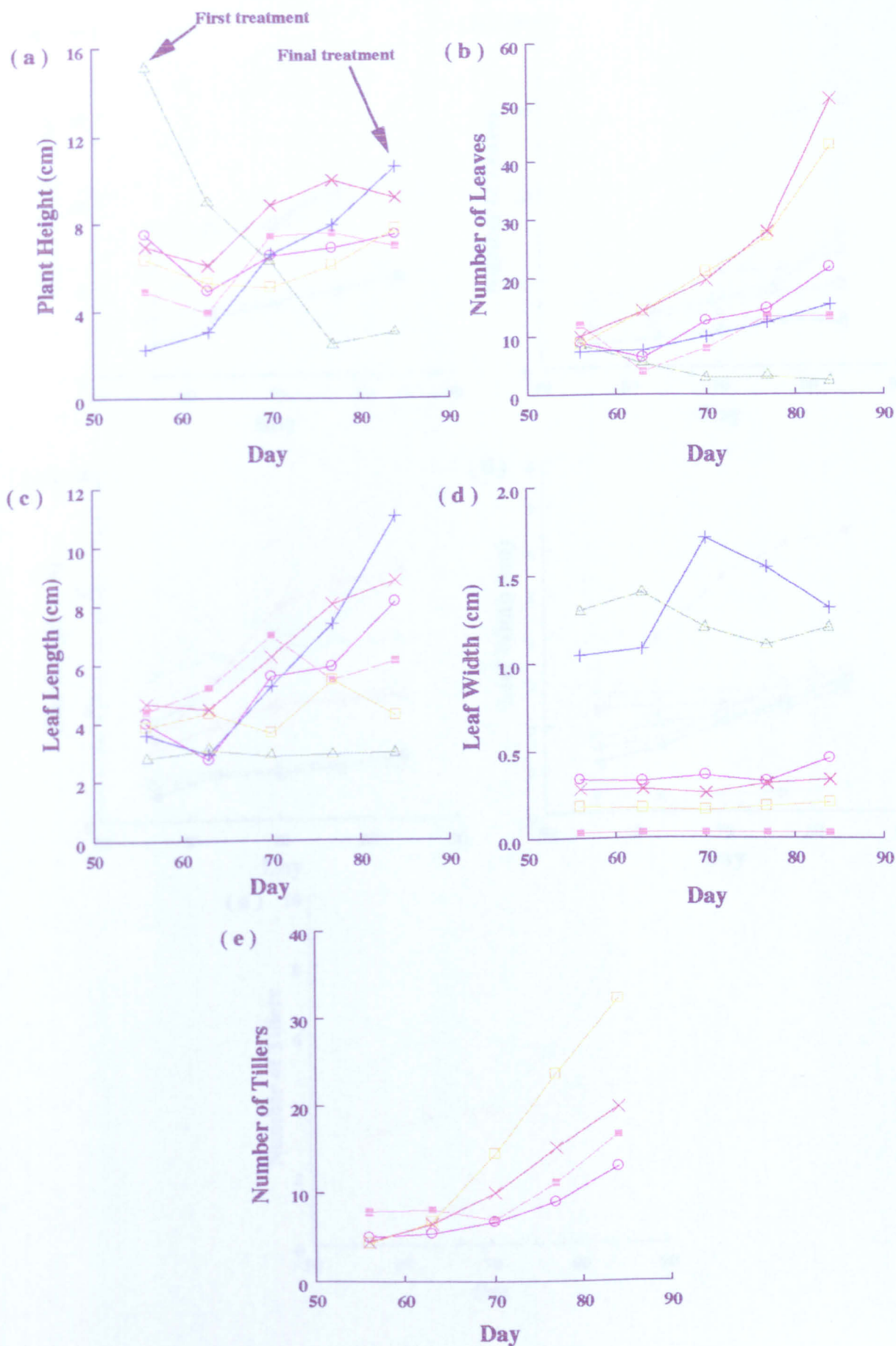


Fig. 4.2 - Growth of morphological parameters over the treatment period for heavily trampled plants of block one (*Plantago lanceolata*; *Deschampsia flexuosa*; *Poa pratensis*; *Holcus lanatus*; *Deschampsia cespitosa* & *Mercurialis perennis*).

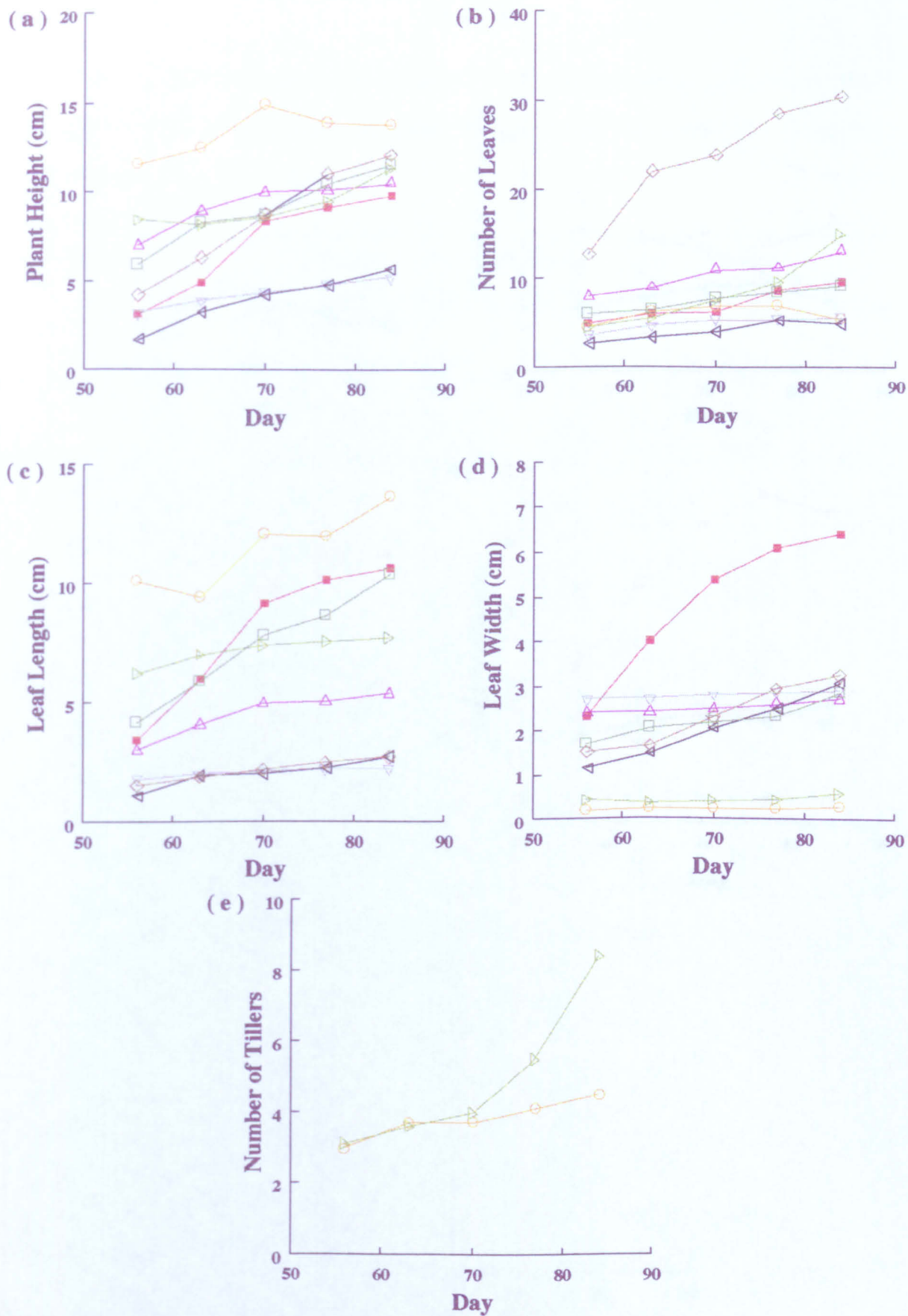


Fig. 4.3 - Growth of morphological parameters over the treatment period for control plants of blocks two and three (*Plantago major*; *Teucrium scorodonia*; *Lolium perenne*; *Brachypodium sylvaticum*; *Geum urbanum*; *Silene dioica*; *Taraxacum officinale* & *Ranunculus ficaria*).

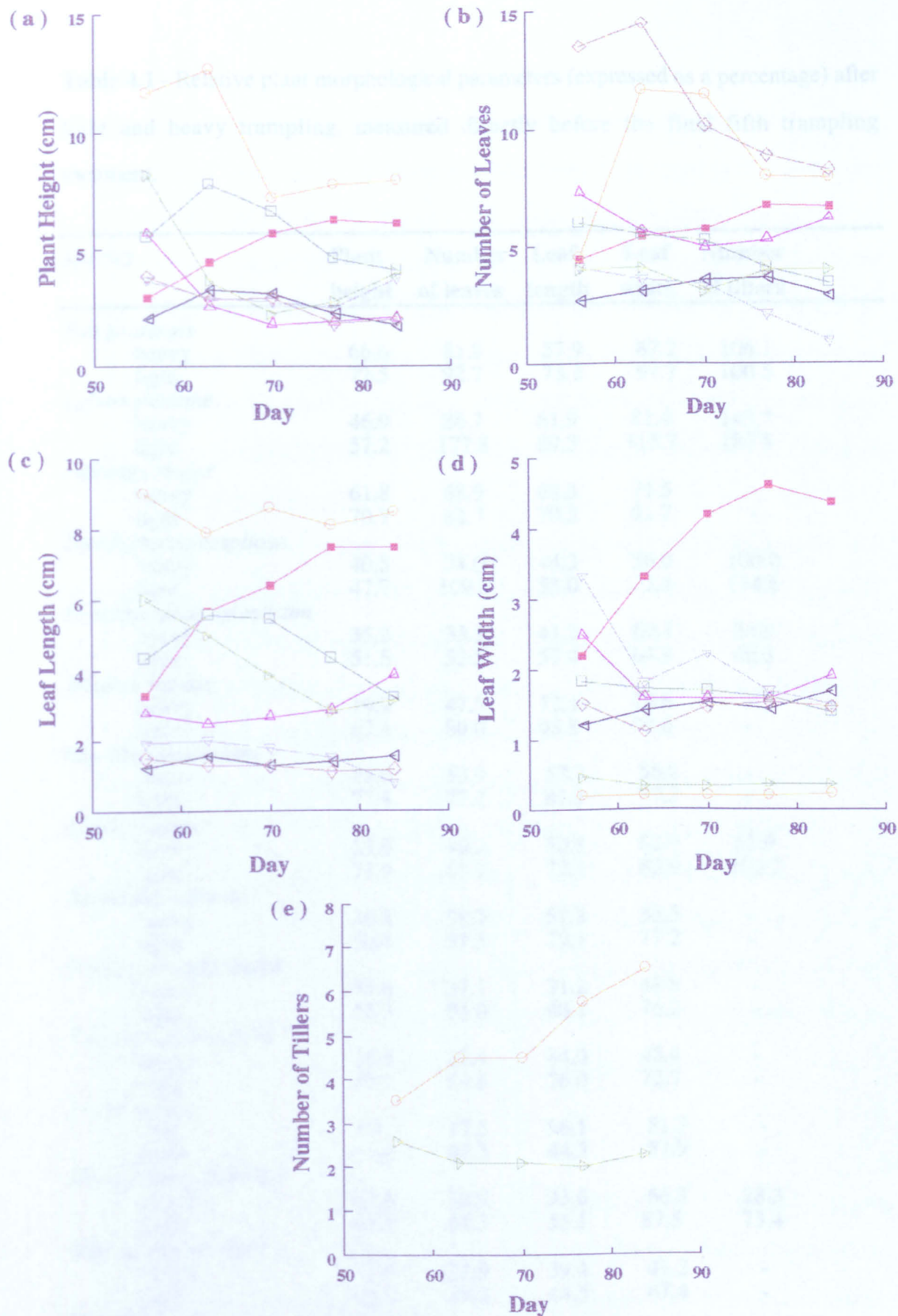


Fig. 4.4 - Growth of morphological parameters over the treatment period for heavily trampled plants of blocks two and three (*Plantago major*; *Teucrium scorodonia*; *Lolium perenne*; *Brachypodium sylvaticum*; *Geum urbanum*; *Silene dioica*; *Taraxacum officinale* & *Ranunculus ficaria*).

Table 4.1 - Relative plant morphological parameters (expressed as a percentage) after light and heavy trampling, measured directly before the final fifth trampling treatment.

<i>Species</i>	Plant height	Number of leaves	Leaf length	Leaf width	Number of tillers
<i>Poa pratensis</i>					
heavy	66.6	81.8	57.9	87.2	106.1
light	72.5	92.7	73.2	97.7	100.5
<i>Lolium perenne</i>					
heavy	46.9	86.7	61.9	81.4	143.7
light	57.2	177.8	89.5	115.7	187.5
<i>Plantago major</i>					
heavy	61.8	68.9	68.3	71.5	-
light	70.7	82.7	70.2	91.7	-
<i>Deschampsia cespitosa</i>					
heavy	40.5	74.0	44.3	56.0	100.0
light	47.7	109.8	53.0	75.4	134.6
<i>Brachypodium sylvaticum</i>					
heavy	35.2	33.3	41.2	60.4	26.9
light	51.5	52.5	57.4	64.9	46.3
<i>Geum urbanum</i>					
heavy	19.9	47.5	72.1	70.6	-
light	67.4	80.0	93.8	92.6	-
<i>Plantago lanceolata</i>					
heavy	59.0	53.9	57.7	56.8	-
light	77.4	77.2	81.1	77.3	-
<i>Holcus lanatus</i>					
heavy	53.9	48.2	50.8	62.9	62.9
light	71.9	85.7	72.1	82.9	103.7
<i>Ranunculus ficaria</i>					
heavy	30.8	58.7	57.3	55.3	-
light	50.4	97.5	79.1	77.2	-
<i>Taraxacum officinale</i>					
heavy	35.6	37.1	31.2	48.8	-
light	56.3	54.0	60.1	76.2	-
<i>Teucrium scorodonia</i>					
heavy	16.5	27.4	44.0	45.4	-
light	48.1	69.6	76.0	72.7	-
<i>Silene dioica</i>					
heavy	7.3	17.5	36.1	51.7	-
light	11.3	41.3	44.3	57.9	-
<i>Deschampsia flexuosa</i>					
heavy	42.6	12.9	33.6	66.7	28.3
light	43.3	61.3	55.1	87.5	73.4
<i>Mercurialis perennis</i>					
heavy	17.4	21.9	39.4	41.2	-
light	28.0	29.2	44.5	47.4	-
F test^a					
heavy	38.9***	120.1***	48.9***	71.3***	619.9***
light	174.3***	504.9***	134.8***	117.9***	2.7*
^a *** significant at 0.001 level					

4.3.1.2 Number of leaves

The number of leaves produced by control plants over the experimental period is variable (Fig. 4.1b & Fig. 4.3b). Many new leaves are synthesised by *Poa pratensis*, *Deschampsia cespitosa* and *D. flexuosa* and *Teucrium scorodonia*. The number of leaves produced by all other species are limited, with *Ranunculus ficaria*, *Silene dioica* and *Lolium perenne* possessing the lowest number of leaves.

Heavy trampling inhibits the production of new leaves in most species (Fig. 4.2b & Fig. 4.4b). Indeed, by the end of the experiment, the number of leaves expressed as a mean of all heavily and lightly trampled species is profoundly reduced to 48 % and 79 % of the control respectively.

The relative number of leaves differs significantly amongst lightly and heavily trampled species (Table 4.1). After heavy trampling, *Poa pratensis*, *Deschampsia cespitosa*, *Plantago major* and *Lolium perenne* have the greatest relative number of leaves, and *Deschampsia flexuosa*, *Teucrium scorodonia*, *Taraxacum officinales*, *Silene dioica*, ~~*Mercurialis perennis*~~ and *Mercurialis perennis* have the lowest.

Thus, vulnerable species undergo a pronounced loss in the relative number of leaves by experiencing substantial defoliation as the treatment period continues. However, light trampling appear to stimulate the capacity of some grasses to induce leaf bearing tillers (section 4.3.1.4), so lightly trampled plants of *Deschampsia cespitosa* and especially *Lolium perenne* have a higher number of leaves than control plants. The relative number of leaves recorded is also high for lightly trampled plants of *Holcus lanatus*, *Geum urbanum*, *Ranunculus ficaria* and *Plantago lanceolata*.

4.3.1.3 Leaf length and width

Leaf lengths increase over the duration of the experimental period in all control plants (Fig. 4.1c & Fig. 4.3c), as do leaf widths (Fig. 4.1d & Fig. 4.3d). Leaf length is greatest and growth most rapid over time for most grass species, *Plantago lanceolata*, *P. major* and *Taraxacum officinales*. In contrast, leaf lengths are lowest in *Teucrium*

scorodonia, *Ranunculus ficaria* and *Silene dioica*. Increases in the widths of leaves are much less obvious in narrow leaved grasses.

The response of leaf lengths (Fig. 4.2c & Fig. 4.4c) and widths (Fig. 4.2d & Fig. 4.4d) to heavy trampling is variable. *Plantago major*, *Lolium perenne*, *Plantago lanceolata*, *Poa pratensis* and *Holcus lanatus* possess the greatest leaf lengths after heavy trampling, showing a progressive increase in leaf length with plant age. *Plantago major* is the only species can increase the width of its leaves under continual heavy trampling. The lowest leaf lengths occur in species which have the poorest control plant growth, namely *Teucrium scorodonia*, *Ranunculus ficaria* and *Silene dioica*. Leaf width declines in *Mercurialis perennis*, *Silene dioica* and *Taraxacum officinale* and remains constant over time for most other species. By the end of the treatment period, the relative leaf length and widths expressed as a mean for heavily trampled species are reduced by half and 64 % compared to the control plants respectively.

The relative leaf lengths and widths of both heavily and lightly trampled plants varies significantly between species (Table 4.1). Heavily trampled *Plantago major*, *Geum urbanum*, *Plantago lanceolata*, *Ranunculus ficaria*, *Poa pratensis* and *Lolium perenne* have the greatest relative leaf lengths, with the latter two species also possessing the greatest relative leaf widths. The lowest relative leaf lengths and widths are recorded in *Teucrium scorodonia* and *Silene dioica*, and most other species have moderate values. The impact of light levels of trampling is far less damaging than heavy trampling, with the mean leaf length and width falling to 68 % and 80 % of the control respectively. The leaf width of lightly trampled plants of *Lolium perenne* is even fractionally greater than the leaf widths of control plants. *Deschampsia flexuosa* has a high relative leaf width, where untrampled leaves are also the thinnest.

4.3.1.4 Number of tillers

The mean number of tillers of control grasses increases with plant age (Fig. 4.1e & Fig. 4.3e). The recruitment of tillers over time occurs most rapidly for grasses in

block one, especially for *Deschampsia flexuosa* and *D. cespitosa*. Tillering is least prolific in the species of block two.

Heavy trampling induces a similar increase in the number of tillers for all species in block one (Fig. 4.2e) and *Lolium perenne* in block two (Fig. 4.4e). Heavy trampling reduces the pooled mean relative number of tillers for the six grasses to 78 % of the control plant species, but light trampling actually increases tillers to 112 % of control plants.

The relative number of tillers of both lightly and heavily trampled species varies significantly between species (Table 4.1), but differences are less significant in the case of lightly trampled plants. After heavy trampling, *Deschampsia flexuosa* and *Brachypodium sylvaticum* have the lowest relative number of tillers, and *Lolium perenne*, *Poa pratensis* and *Deschampsia cespitosa* have the greatest relative number. Light levels of trampling stimulate tiller production of *Lolium perenne*, where almost twice the amount of tillers are produced by trampled plants. The number of tillers are also higher or equal to the number of tillers produced by control plants for *Deschampsia cespitosa*, *Poa pratensis* and *Holcus lanatus*.

4.3.2 Biomass

The above- and below ground biomass are greatest in control plants, intermediate in lightly trampled plants and lowest in heavily trampled plants (Table 4.2). Above- and below ground biomass generally differ significantly between trampling treatments in the majority of cases. Total biomass is higher for species of block one compared to the other blocks.

Table 4.2 - The mean biomass (g per individual) for sixteen species measured two days after the final trampling treatment, and results of one-way ANOVA tests to compare biomass (g per individual) between the control, light and heavy levels of simulated trampling for each species.

<i>Species</i>	<u>Mean biomass (g per individual)</u>			F-test^a
	Control	Light	Heavy	
<i>Poa pratensis</i>				
above-ground	5.90	5.07	4.07	57.4***
below-ground	38.14	15.19	10.98	190.8***
<i>Deschampsia cespitosa</i>				
above-ground	8.96	5.79	3.60	210.0***
below-ground	26.71	10.03	5.89	95.3***
<i>D. flexuosa</i>				
above-ground	1.94	0.62	0.05	402.3***
below-ground	3.61	0.76	0.36	113.3***
<i>Holcus lanatus</i>				
above-ground	9.22	5.00	2.11	951.7***
below-ground	12.98	11.40	1.37	92.84***
<i>Plantago lanceolata</i>				
above-ground	7.22	3.25	1.84	104.9***
below-ground	5.79	3.81	2.27	28.1***
<i>Mercurialis perennis</i>				
above-ground	1.73	0.05	0.02	116.5***
below-ground	1.20	0.26	0.21	65.3***
<i>Taraxacum officinale</i>				
above-ground	0.37	0.15	0.08	59.9***
below-ground	0.10	0.06	0.02	116.2***
<i>Teucrium scorodonia</i>				
above-ground	1.58	0.90	0.21	121.3***
below-ground	0.75	0.34	0.11	99.8***
<i>Lolium perenne</i>				
above-ground	0.20	0.15	0.10	6.2*
below-ground	0.04	0.04	0.03	1.5
<i>Brachypodium sylvaticum</i>				
above-ground	0.26	0.09	0.07	8.4*
below-ground	0.14	0.07	0.05	51.8***
<i>Geum urbanum</i>				
above-ground	0.21	0.10	0.06	20.1**
below-ground	0.10	0.05	0.02	73.5***
<i>Silene dioica</i>				
above-ground	0.50	0.18	0.06	43.5***
below-ground	0.09	0.05	0.03	36.3***
<i>Oxalis acetosella</i>				
above-ground	0.13	-	-	-
below-ground	0.04	-	-	-
<i>Anemone nemorosa</i>				
above-ground	0.25	-	-	-
below-ground	0.27	-	-	-
<i>Plantago major</i>				
above-ground	4.70	2.83	1.97	2.88
below-ground	1.79	0.68	0.52	69.5***

Species	Mean biomass (g per individual)			F-test ^a
	Control	Light	Heavy	
<i>Ranunculus ficaria</i>				
above-ground	0.17	0.07	0.03	15.9**
below-ground	0.23	0.09	0.07	56.6***

^a - * significant at 0.05 level; ** significant at 0.01 level; *** significant at 0.001 level

Above-ground biomass combined for all species that survived the trampling treatment differed significantly between simulated trampling treatments (Table 4.3). The level of significance diminishes as recovery time increases after the final treatment. Multiple comparisons also reveal that 30 days after the final treatment, the biomass of lightly trampled and control plants are similar.

Table 4.3 - One-way ANOVA and Tukey HSD of combined species above-ground biomass at each of the four biomass harvests showing differences between control, light and heavy simulated trampling treatments.

Biomass harvest	Days after last treatment	df	F-test	p	Tukey HSD ^a
1	2	125	7.65	0.001	C > (L, H)
2	16	125	6.69	0.002	C > (L, H)
3	30	125	6.07	0.003	(C > H), L
4	44	125	5.40	0.006	(C > H), L

^a - significant at $p \leq 0.05$; C = control (zero drops), L = light trampling (10 tramples per week), H = heavy trampling (30 tramples per week).

The relative above-ground biomass of heavily trampled plants generally undergoes a slight increase as the recovery period continues, but there is much variability between species (Fig. 4.5). Recovery of biomass is greatest in *Deschampsia cespitosa* (Plate 4.1), *Plantago major*, *Plantago lanceolata* and *Taraxacum officinale* (Plate 4.2). *Geum urbanum* and *Holcus lanatus* show no net recruitment in biomass over the recovery period, whereas *Ranunculus ficaria* undergoes a decline in relative biomass. Differences amongst species are significant at both simulated trampling levels two

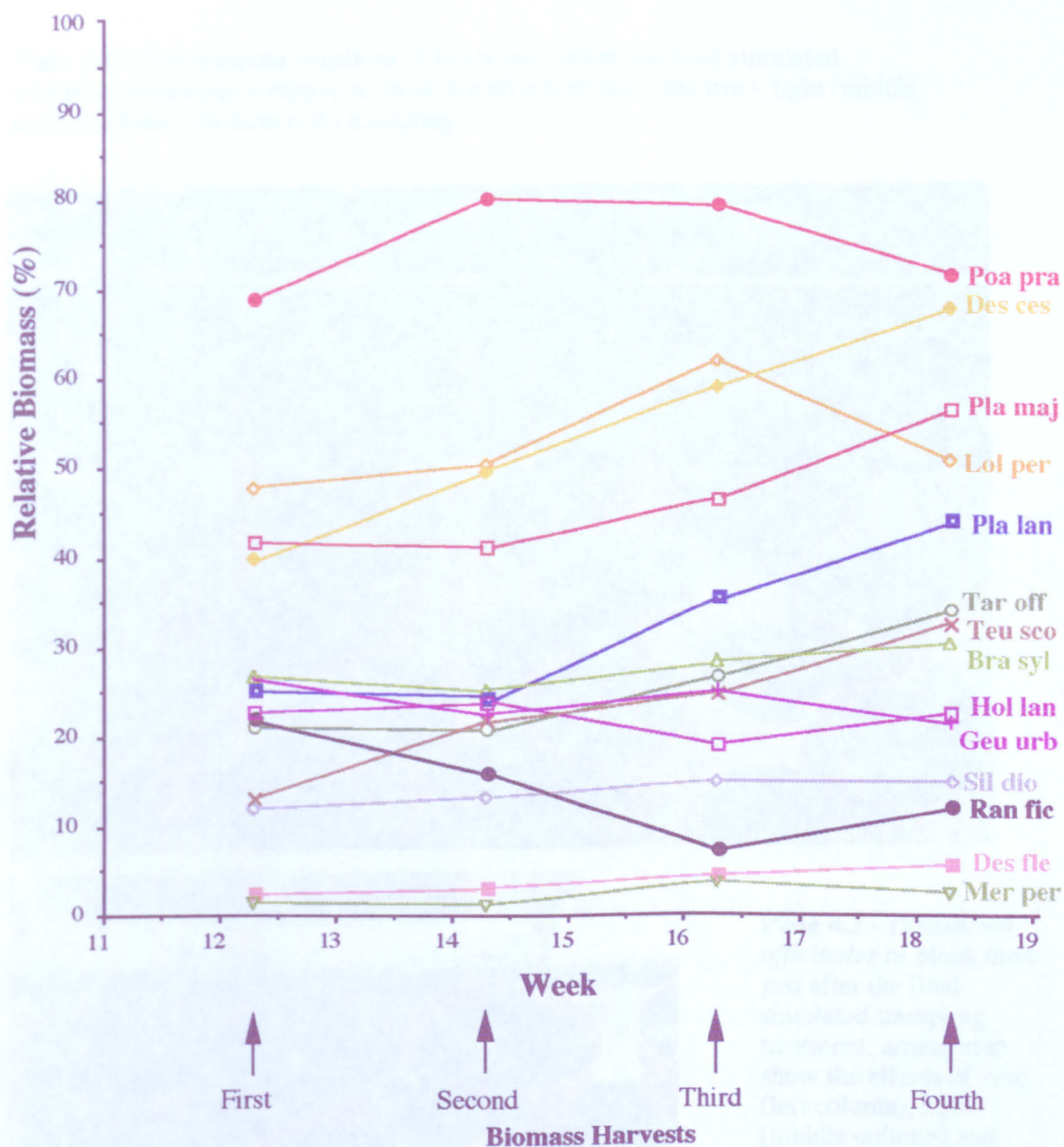


Fig. 4.5 - Relative biomass recorded for all fourteen species that survived the simulated heavy trampling treatment (30 tamp drops per week for 5 weeks from week 8 until week 12). The first biomass harvest (the resistance index) was taken two days after the final trampling treatment, and the others at subsequent two week intervals. *Poa pra* - *Poa pratensis*; *Des ces* - *Deschampsia cespitosa*; *Lol per* - *Lolium perenne*; *Pla maj* - *Plantago major*; *Pla lan* - *Plantago lanceolata*; *Tar off* - *Taraxacum officinales*; *Teu sco* - *Teucrium scorodonia*; *Sil dio* - *Silene dioica*; *Geu urb* - *Geum urbanum*; *Ran fic* - *Ranunculus ficaria*; *Des fle* - *Deschampsia flexuosa*; *Bra syl* - *Brachypodium sylvaticum*; *Hol lan* - *Holcus lanatus* & *Mer per* - *Mercurialis perennis*.

Plate 4.1 - *Deschampsia cespitosa* of block one before the final simulated trampling treatment, arranged to show the effects of zero (top row), light (middle row) and heavy (bottom row) trampling



Plate 4.2 - *Taraxacum officinale* of block three just after the final simulated trampling treatment, arranged to show the effects of zero (left column), light (middle column) and heavy (right column) trampling

days after the final trampling treatment (heavy: $F = 13.8$, $p \leq 0.001$; light: $F = 7.7$, $p \leq 0.001$).

In response to heavy trampling, *Poa pratensis*, *Lolium perenne*, *Deschampsia cespitosa* and *Plantago major* are highly resistant, *Geum urbanum* has moderate resistance (Plate 4.3a), whilst *Teucrium scorodonia* and *Silene dioica* (Plate 4.3b) have low resistances. *Deschampsia flexuosa* and *Mercurialis perennis* have very low resistance and the remaining species are moderately resistant. Light trampling generally has a less damaging impact, with *Mercurialis perennis* the only species with a low resistance.

Fig. 4.6 and Fig. 4.7 shows the differences in relative above- and below-ground biomass respectively in light and heavy trampling. The growth of below-ground biomass is stringently restricted by pot size, so below-ground biomass is not utilised as an trampling indicator. Even so, below-ground biomass declines as trampling intensity increases.

The regression models generated to approximate the relationship between time and the natural logarithm of control above-ground plant biomass (relative growth rate) are significant for most species (Table 4.4). Differences between the relative growth rates of species are highly significant ($F = 15.4$; $p \leq 0.001$). *Brachypodium sylvaticum* has a high relative growth rate, *Deschampsia flexuosa*, *Taraxacum officinale*, *Lolium perenne* and *Ranunculus ficaria* have moderate growth rates whilst the growth rates of the remaining species are low.

For the majority of species, regressions modelling the relationship between the natural logarithm of lightly and heavily trampled above-ground plant biomass (relative recovery rates) with time are significant (Table 4.4). Relative recovery rates also differ significantly between species (heavy relative recovery rate: $F = 7.3$, $p \leq 0.001$; light relative recovery rate: $F = 6.6$, $p \leq 0.001$).

Plate 4.3 - Single specimens of block three collected before the first biomass harvest, showing size differences between heavily (left), lightly (middle) and control (right) trampled plants, for (a). *Geum urbanum*



(b). *Silene dioica*



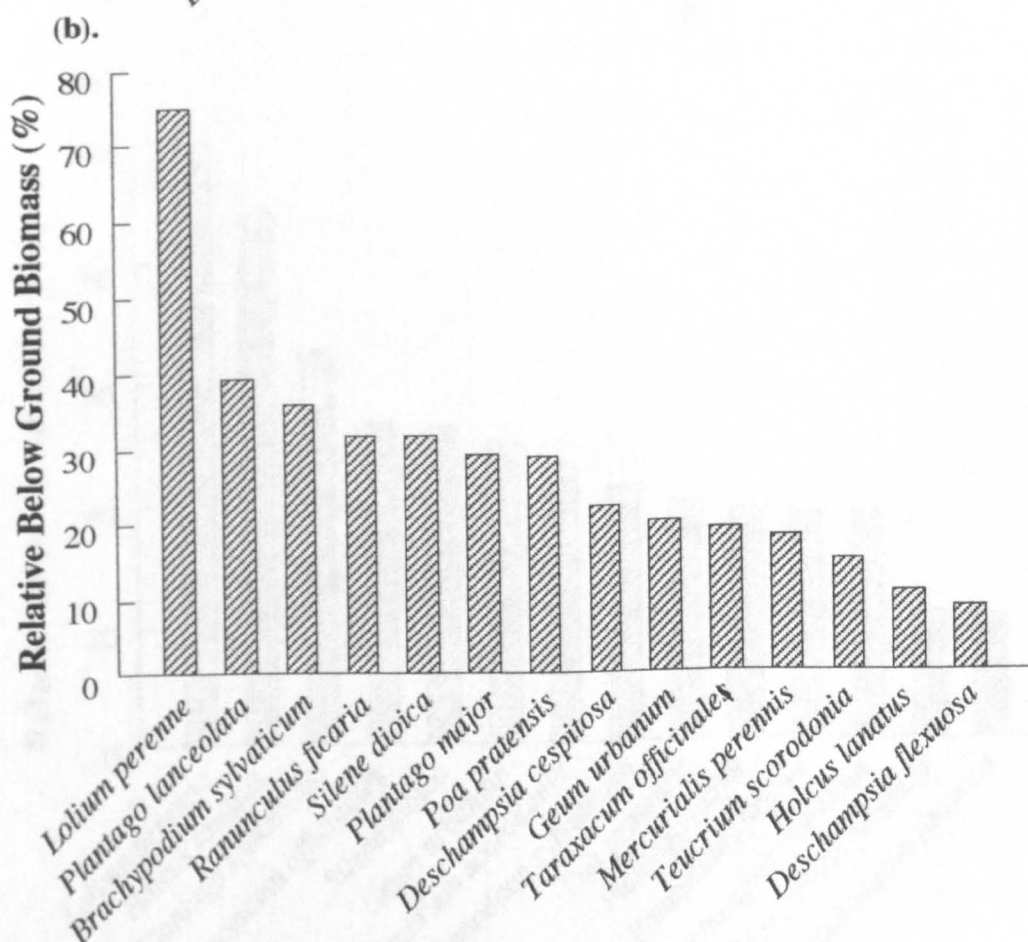
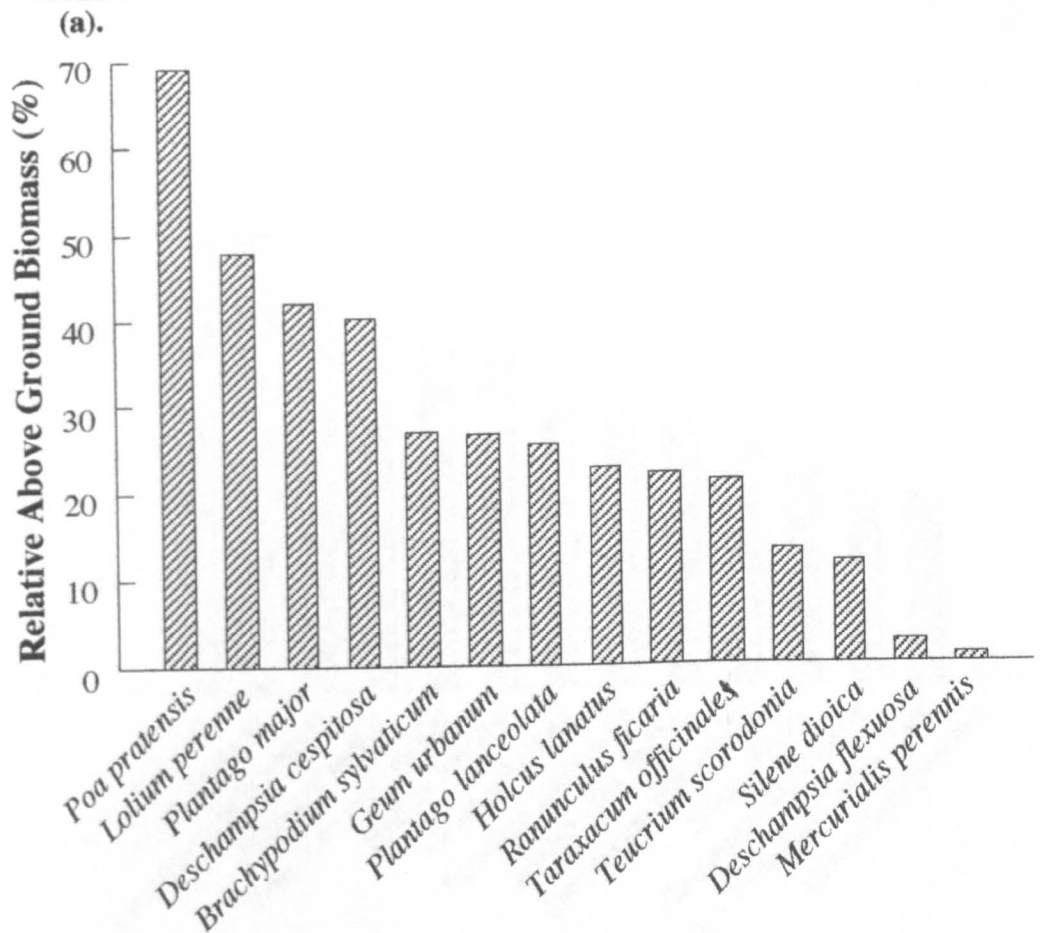


Fig. 4.6 - The (a). relative above ground biomass (resistance index) and (b). relative below ground biomass of **heavily** trampled species. Biomass harvests were collected two days after the final trampling treatment.

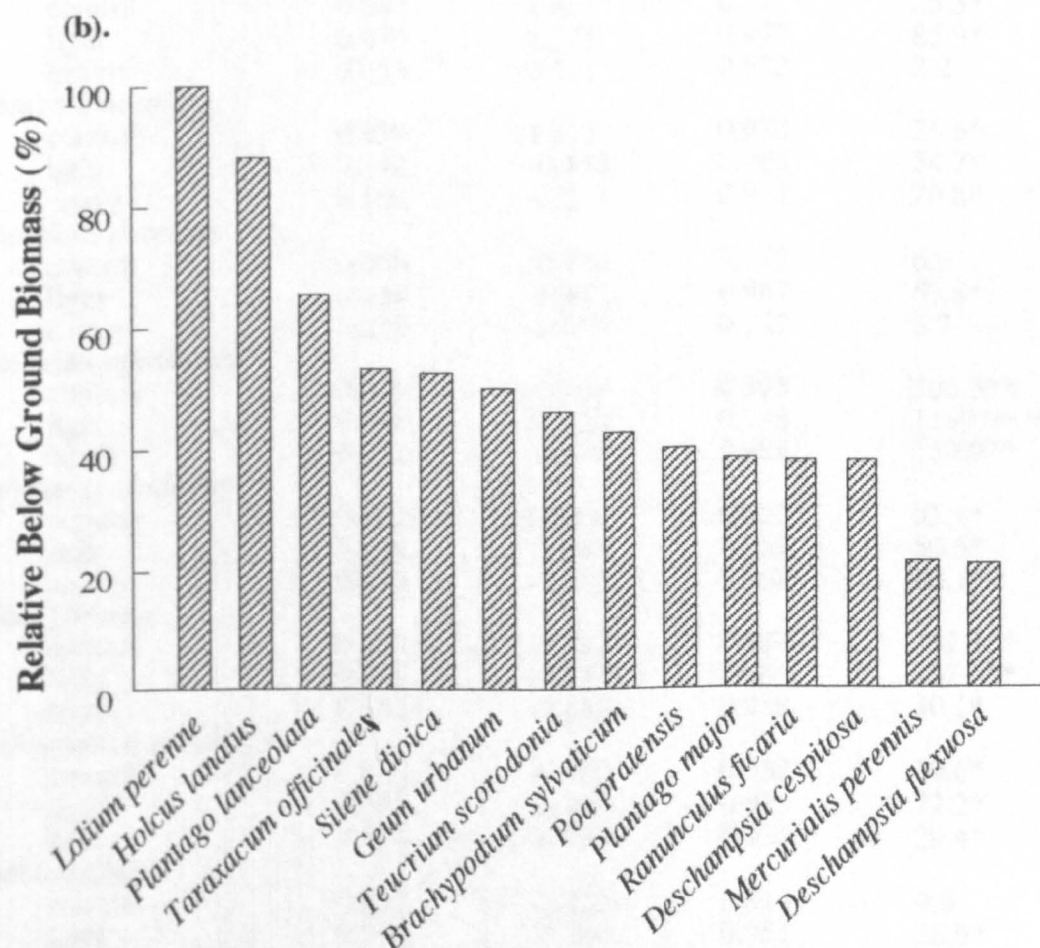
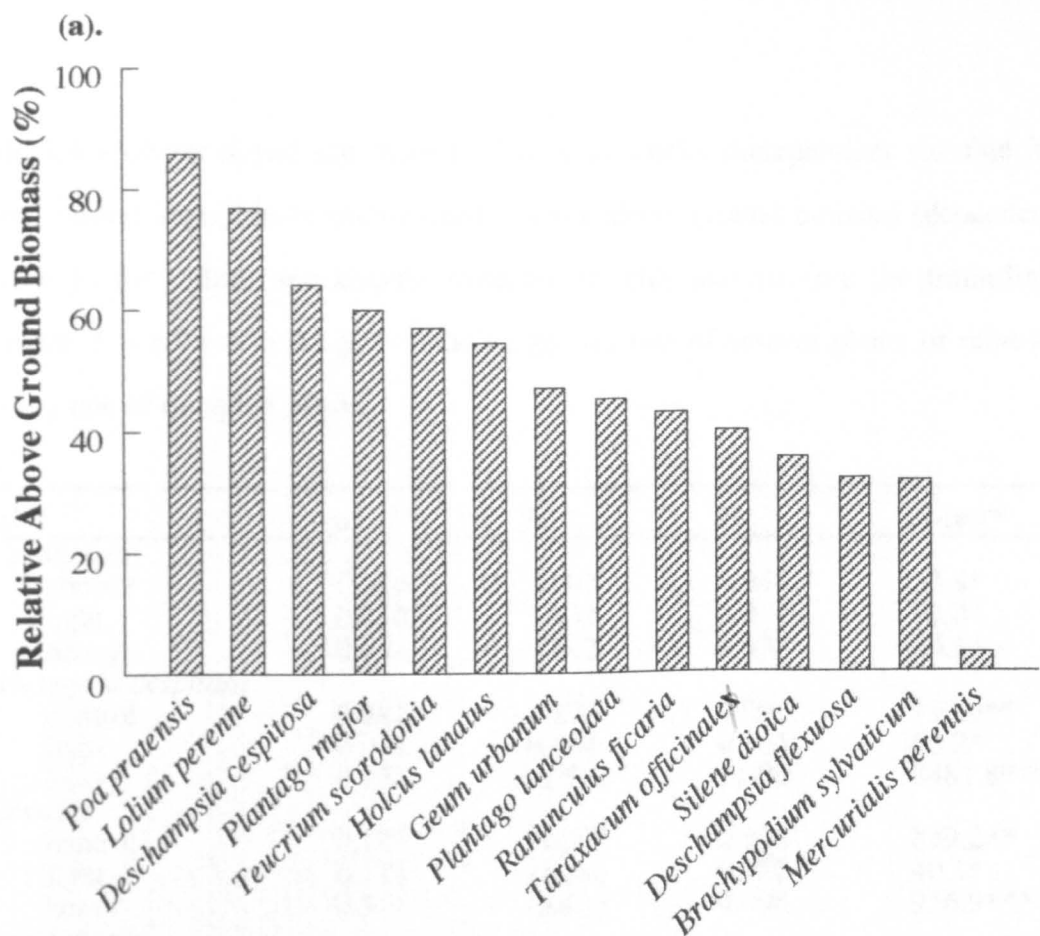


Fig. 4.7 - The (a). relative above ground biomass and (b). relative below ground biomass of **lightly** trampled species. Biomass harvests were collected two days after the final trampling treatment.

Table 4.4 - Linear regression models of time in weeks (independent variable X) against natural logarithm of transformed relative above-ground biomass (dependent variable Y) for lightly and heavily trampled species that survive the trampling treatment. $Y = aX + b$; a (slope) = relative growth rate of control plants or relative recovery rate of trampled plants.

Species	a	b	r^2	F -test ^a
<i>Poa pratensis</i>				
control	0.059	1.097	0.944	33.8*
light	0.052	1.037	0.974	75.0*
heavy	0.064	0.742	0.936	29.1*
<i>Deschampsia cespitosa</i>				
control	0.082	1.270	0.990	193.9**
light	0.098	0.604	0.965	55.2*
heavy	0.168	-0.567	1.000	8481.8***
<i>D. flexuosa</i>				
control	0.177	-1.297	0.998	859.2**
light	0.178	-2.381	0.952	40.1*
heavy	0.311	-6.425	0.998	956.9***
<i>Holcus lanatus</i>				
control	0.067	1.451	0.927	25.3*
light	0.079	0.725	0.977	85.9*
heavy	0.053	0.121	0.522	2.2
<i>Plantago lanceolata</i>				
control	0.059	1.313	0.930	26.6*
light	0.142	-0.430	0.965	54.7*
heavy	0.160	-1.257	0.931	26.8*
<i>Mercurialis perennis</i>				
control	0.066	-0.188	0.775	6.9
light	0.224	-5.421	0.967	57.8*
heavy	0.228	-6.509	0.742	5.7
<i>Taraxacum officinale</i> †				
control	0.149	-2.793	0.995	596.3**
light	0.188	-4.223	0.998	1189.9***
heavy	0.232	-5.448	0.988	159.9**
<i>Teucrium scorodonia</i>				
control	0.032	0.053	0.963	52.1*
light	0.134	-1.540	0.962	50.6*
heavy	0.173	-3.389	0.968	60.1*
<i>Lolium perenne</i>				
control	0.110	-2.782	0.987	152.1**
light	0.151	-3.533	0.985	132.6**
heavy	0.126	-3.668	0.938	30.1*
<i>Brachypodium sylvaticum</i>				
control	0.330	-5.108	0.952	39.6*
light	0.387	-6.759	0.973	72.2*
heavy	0.354	-6.759	0.936	29.4*
<i>Geum urbanum</i>				
control	0.072	-2.422	0.819	9.0
light	0.140	-3.180	0.951	38.9*
heavy	0.046	-3.493	0.509	2.1

Species	<i>a</i>	<i>b</i>	<i>r</i> ²	<i>F</i> -test ^a
<i>Silene dioica</i>				
control	0.087	-1.634	0.991	222.4**
light	0.095	-2.780	0.975	77.9*
heavy	0.126	-4.171	0.973	72.2*
<i>Plantago major</i>				
control	0.072	0.731	0.977	83.3*
light	0.102	-0.187	0.862	12.5
heavy	0.123	-0.758	0.930	26.7*
<i>Ranunculus ficaria</i>				
control	0.171	-2.663	0.752	6.1
light	0.099	-3.205	0.780	7.1
heavy	-0.011	-1.584	0.023	0.05

^a - * significant at 0.05 level; ** significant at 0.01 level; *** significant at 0.001 level

The relative recovery rates of *Brachypodium sylvaticum*, *Deschampsia flexuosa*, *Mercurialis perennis* and *Taraxacum officinale* are high after heavy trampling. However, recovery rates are low for *Geum urbanum*, *Holcus lanatus*, *Poa pratensis* and *Ranunculus ficaria*, and moderate in all other species. With the exception of *Ranunculus ficaria*, *Geum urbanum* and *Holcus lanatus*, the relative recovery rates in response of species to heavy trampling are generally greater than their respective relative recovery rates to light trampling. Accordingly, the ratio of the relative recovery rate to the relative growth rate is lowest for the aforementioned three species, and highest for *Teucrium scorodonia*, *Mercurialis perennis*, *Plantago lanceolata*, *Deschampsia cespitosa*, *D. flexuosa* and *Plantago major*.

An arbitrary classification table of relative growth rates, and resistance to and recovery from light and heavy trampling is presented for species in Table 4.5. It is evident that species of high resistance tend to possess low or moderate growth and recovery rates, whereas species of low resistance have variable recovery rates.

Table 4.5 - Classification of the sixteen species according to the results of Tukey HSD tests for relative growth rate, relative recovery rates and resistance indices to light and heavy trampling.

<i>Species</i>	Resistance	Relative growth rate	Relative recovery rate
<i>Poa pratensis</i>			
heavy	high	low	low
light	high		low
<i>Lolium perenne</i>			
heavy	high	moderate	moderate
light	high		moderate
<i>Plantago major</i>			
heavy	high	low	moderate
light	high		moderate
<i>Deschampsia cespitosa</i>			
heavy	high	low	moderate
light	high		moderate
<i>Brachypodium sylvaticum</i>			
heavy	moderate	high	high
light	moderate		high
<i>Geum urbanum</i>			
heavy	moderate	low	low
light	moderate		moderate
<i>Plantago lanceolata</i>			
heavy	moderate	low	moderate
light	moderate		moderate
<i>Holcus lanatus</i>			
heavy	moderate	low	low
light	high		low
<i>Ranunculus ficaria</i>			
heavy	moderate	moderate	low*
light	moderate		moderate
<i>Taraxacum officinale</i>			
heavy	moderate	moderate	high
light	moderate		moderate
<i>Teucrium scorodonia</i>			
heavy	low	low	moderate
light	moderate		moderate
<i>Silene dioica</i>			
heavy	low	low	moderate
light	moderate		moderate
<i>Deschampsia flexuosa</i>			
heavy	low	moderate	high
light	moderate		moderate
<i>Mercurialis perennis</i>			
heavy	low	low	high
light	low		high

* - negative

The nature of the relationships between the resistance indices, relative growth rate and relative recovery rates are presented in Table 4.6. Correlations between relative

growth rate and relative recovery rates are positive and significant at both levels of trampling. All other correlations are negative and non-significant, but the correlations between the resistance index and the relative recovery rates are high (heavy trampling: $p \leq 0.20$; light trampling: $p \leq 0.10$).

Table 4.6 - Pearson correlation coefficients (r)^{to illustrate inter-species relationships} between resistance indices, relative growth rate and relative recovery rates for lightly and heavily trampled species.

Comparison	N	HEAVY	LIGHT
resistance index vs. relative recovery rate	14	-0.39	-0.52
resistance index vs. relative growth rate	14	-0.13	-0.27
relative recovery rate vs. relative growth rate	14	0.55*	0.77**

N = number of species; * - significant at $p \leq 0.05$, ** - significant at $p \leq 0.01$.

4.3.3 The impact of shade

4.3.3.1 Morphological parameters

The height of control plants increases gradually with plant age in all three species under the shady conditions of block four (Fig 4.8a). However, plants of *Plantago major* in block three are almost twice as tall. The opposite is the case for control plants of *Silene dioica*, and the response of control plants of *Geum urbanum* under the two light climates is similar.

Heavy trampling severely reduces plant height in *Geum urbanum* and *Silene dioica* (Fig. 4.8a), and subdues the ability of *Plantago major* to increase height over the experimental period. The number of leaves produced by all three species increase over time (Fig. 4.8b), but the species of block four produce fewer leaves than those of block three. Heavy trampling promotes a cumulative decline in the number of leaves

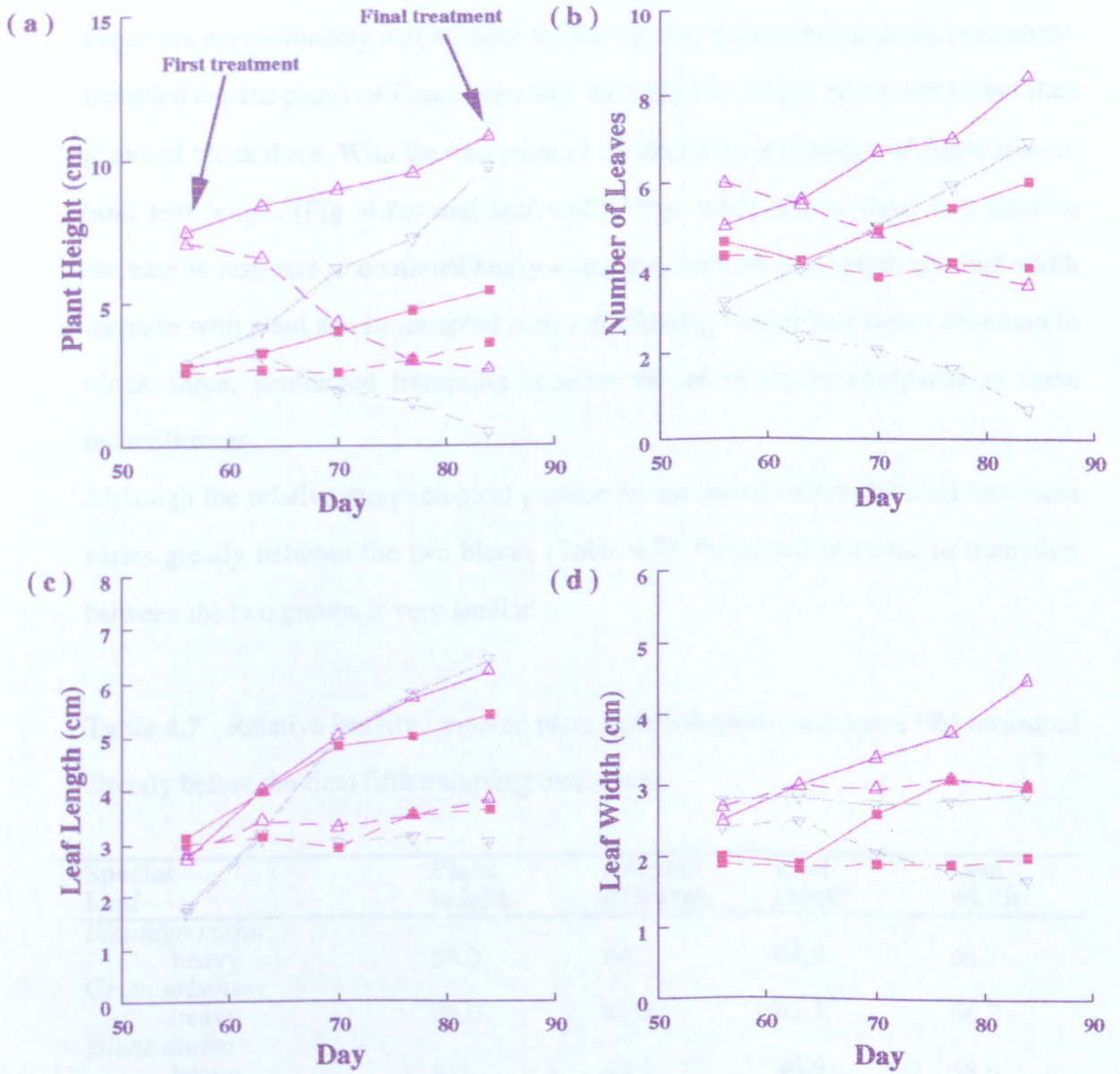


Fig. 4.8 - Growth of morphological parameters over the treatment period for heavily trampled plants (dashed lines) and control plants (solid lines) of block four. (*Geum urbanum*, *Plantago major*, *Silene dioica*).

of *Silene dioica* and *Geum urbanum* (Fig. 4.8b), and leaf production is very much subdued in *Plantago major*.

Both leaf length (Fig. 4.8c) and leaf width (Fig. 4.8d) increase with plant age in shaded species, but by the end of the experiment, leaf lengths and widths of *Plantago major* are approximately half of those for the same species in block three. In contrast, trampled shaded plants of *Geum urbanum* have slightly longer and wider leaves than plants of block three. With the exception of the declining leaf length of *Silene dioica*, both leaf length (Fig. 4.8c) and leaf width (Fig. 4.8d) fail to show any relative increase in response to continual heavy trampling. As both leaf length and leaf width increase with plant age in trampled plants of *Plantago major* and *Geum urbanum* in block three, prolonged trampling is more severe in shady compared to open microclimates.

Although the relative morphological parameters measured before the final treatment varies greatly between the two blocks (Table 4.7), the actual response to trampling between the two groups is very similar.

Table 4.7 - Relative heavily trampled plant morphological parameters (%) measured directly before the final fifth trampling treatment.

Species Leaf	Plant height	Number of leaves	Leaf length	Leaf width
<i>Plantago major</i> heavy	59.2	66.7	64.8	66.7
<i>Geum urbanum</i> heavy	25.0	42.9	61.3	66.7
<i>Silene dioica</i> heavy	5.0	10.1	46.9	58.6

4.3.3.2 Biomass

The above- and below-ground biomass measured two days after the final trampling treatment is greatest in control plants and lowest in heavily trampled plants, with the above-ground biomass differing significantly between the trampling treatments (Table 4.8).

Above-ground biomass of control and heavily trampled *Plantago major* in block three are significantly higher than in block four (Table 4.8). The above-ground biomass for control plants of *Silene dioica* in block three are also significantly greater than those in block four. For all species, blocks three and four are similar in terms of their heavily trampled relative biomass measured two days after the final trampling treatment ('resistance index').

Table 4.8 - The mean biomass (g per individual) of the three species two days after the final trampling treatment. Paired t-tests compare the control and heavy trampling above-ground plant biomass, and comparisons of the above-ground biomass and the resistance index of 'shade' plants of block four with 'sun' plants of block three.

<i>Species</i>	<u>Simulated Trampling Level</u>			<u>Light Vs Shade</u>		
	Control	Heavy	<i>t</i>	Control <i>t</i>	Heavy <i>t</i>	<i>Resistance t</i>
<i>Plantago major</i>						
above-ground	0.94	0.37	15.6**	-12.7**	-8.8*	1.7
below-ground	0.36	0.08				
<i>Geum urbanum</i>						
above-ground	0.26	0.13	7.8*	-3.2	-0.2	0.6
below-ground	0.05	0.05				
<i>Silene dioica</i>						
above-ground	1.01	0.085	11.3**	9.0*	-1.9	0.4
below-ground	0.095	0.03				

* - significant at 0.05 level, ** - significant at 0.01 level.

The linear regression models generated for each species in block four illustrate the relationship between recovery time and the natural logarithm of above-ground biomass (Table 4.9). Relative growth rates and relative recovery rates are both negative for *Plantago major*.

Table 4.9 - Linear regression models of time in weeks (independent variable X) against natural logarithm of transformed relative biomass (dependent variable Y) for heavily trampled shaded species that survive the trampling treatment. $Y = aX + b$; a (slope) = relative growth rate of control plants or relative recovery rate of trampled plants.

<i>Species</i>	<i>a</i>	<i>b</i>	r^2	<i>F</i> -test ^a
<i>Plantago major</i>				
control	-0.004	0.028	0.060	0.1
heavy	-0.020	-0.739	0.690	4.4
<i>Geum urbanum</i>				
control	0.041	-1.870	0.970	66.0*
heavy	0.044	-3.540	0.790	7.6
<i>Silene dioica</i>				
control	0.081	-3.600	0.640	3.5
heavy	0.069	-3.440	0.600	3.0

^a - * significant at 0.05 level

The relative growth rate regression coefficients of *Plantago major* and *Silene dioica* in blocks four and three differ significantly (Table 4.10).

Table 4.10 - A comparison between the 'sun' and 'shade' linear regression coefficients obtained from blocks three and four respectively for the relative growth rate of control plants and the relative recovery rate of heavily trampled plants.

<i>Species</i>	<i>v</i>	<i>t</i>	<i>p</i>
<i>Plantago major</i>			
relative growth rate	4	23.8	***
relative recovery rate	4	0.5	NS
<i>Geum urbanum</i>			
relative growth rate	4	0.5	NS
relative recovery rate	4	0.01	NS
<i>Silene dioica</i>			
relative growth rate	4	2.9	*
relative recovery rate	4	0.01	NS

v = combined residual degrees of freedom; NS - not significant, * - significant at 0.05 level, *** - significant at 0.001 level.

This suggests that shade reduces the growth rate of species that are intolerant of shade relative to their response in open microclimates. No differences were apparent for the shade tolerant *Geum urbanum*. Relative recovery rates from heavy trampling did not differ significantly between plants of block three and those of block four, implying that the impact of heavy trampling was sufficiently damaging for microclimate to be irrelevant.

Chapter 5

**THE IMPACT OF RECREATIONAL TRAMPLING
ON WOODLAND SOILS**

5.1 Introduction

The number of studies examining recreational trampling on woodland soils in Britain is rather limited (Anderson & Radford 1992, Bryan 1977), and the affect of trampling on forest soils is poorly understood (Cole pers. commn 1995). This chapter addresses these shortcomings by quantifying the response of soil characteristics to trampling, and supplements the preliminary monitoring of woodland soils undertaken in Chapter 2.

5.1.1 Research proposals

- To monitor seasonal fluctuations in soil parameters of surface and sub-surface soils located on and off trails in three woodland sites.
- To model the nature of the relationship between soil parameters and trampling intensity, and to examine inter-relationships between soil physical and chemical parameters whilst relating both to soil type and structure, drainage patterns and forces of erosion.
- To further the understanding of the response of soil parameters to recreational trampling in order to promote the conservation of soils in recreation sites.
- To generate management criteria that will help resource managers locate, *develop, maintain and rehabilitate* trails on medium to heavily textured woodland soils.

5.2 Materials and methods

5.2.1 *Fieldwork sites*

Detailed site and soil descriptions for the Tilehill and Tocil Woods are provided in Table 2.1.

5.2.2 *Extraction of samples*

The response of woodland soils to long-term trampling was investigated along established woodland rides, tracks and footpaths. Soil samples were removed in discrete sampling blocks. To provide contrasting sites for the sampling blocks, study trails were subjectively divided into one of four wear class zones. The wear class zones ran perpendicular to the line of wear and consisted of a heavily trampled central zone, two adjacent moderately trampled zones, two further adjacent trailside lightly trampled zones and an untrampled control zone located at least two metres from the trailside. Any differences in the physical condition of the soil between the path and the surrounds were as a direct result of trampling pressure, and reflected the deterioration in comparison with controls. This assumed that there was a gradient of pressure from the centre outwards, and that the soil was at equilibrium with the pressure (Goldsmith 1974).

Woodland soils are difficult to sample because of coarse fragments and abundant tree roots (Fleming *et al.* 1993, Payne pers. commn 1994). Accordingly, undisturbed surface samples were obtained by excavation using a root auger of 10 cm diameter and 10 cm depth in each wear class. An open ended metal cylinder of 3.8 cm diameter and 23 cm length was then manually driven into the exposed lower soil horizons using a soil corer. Samples were later removed from their cylinders using a hand operated extruder (available from ELE International Ltd, Hertfordshire, England).

5.2.3 *Frequency of sampling*

Three discrete samples were collected from each sampling block, with each sample consisting of a further three surface (0 to 10 cm depth) and sub-surface (10 to 30 cm depth) replicates extracted from each of the four wear classes. The bulked or composite sampling technique described by Smith & Atkinson (1975) was used to aggregate samples. Thirteen sampling blocks were carried out at irregular intervals in Tocil Wood and seven in Tilehill Wood between September 1994 and March 1996. Six blocks were carried out in Crackley Wood between November 1995 and February 1997.

5.2.4 *Soil physical and chemical tests*

Methodology was adapted from procedures outlined by Rowell (1994), Avery (1990) and Smith & Atkinson (1975).

5.2.4.1 *Bulk density*

An infill method was used to estimate the bulk density of surface soils (British Standards Institution 1967). After the removal of surface soil plugs, individual soil pits were lined with plastic bags and filled with fine sand. The sand was levelled flush with the ground surface, and the soil volume was calculated as the volume of sand required to fill the excavated hole. The surface and sub-surface soil samples were weighed, oven dried overnight at 105°C and reweighed. Bulk density was expressed in ' g cm⁻³ ', and was defined as the mass of oven-dry soil divided by the volume of the excavated pit or volume of the cylinder.

5.2.4.2 *Particle density*

25 g of oven-dry soil from each surface and sub-surface replicate sample was gently boiled with 50 ml of distilled water for 45 minutes. The suspension was allowed to cool and poured into a pre-weighed 125 ml specific gravity bottle that was topped up to capacity with distilled water, and then reweighed. The density of particles was the

mass of dry soil divided by the volume of particles in the bottle, expressed in 'g cm⁻³'.

5.2.4.3 *Total porosity*

The amount of particles in 1 cm³ of soil was the bulk density multiplied by one and divided by the particle density. The total porosity was one minus this value, expressed in 'cm³ pores cm⁻³ soil' and multiplied by 10² to be expressed as a volume ratio.

5.2.4.4 *Gravimetric and volumetric water content*

20 g of fresh surface or sub-surface bulked soil was weighed, and left to dry in an oven at 105°C overnight. Samples were then reweighed. Gravimetric water content was expressed in 'g H₂O g⁻¹ soil' and was calculated for each sampling block by dividing the bulked oven-dry mass of soil into the bulked fresh mass of soil. The volumetric water content per sampling block was expressed in 'cm³ H₂O cm⁻³ soil'. and was calculated by multiplying the gravimetric water content values by their paired mean bulk density values in each wear class.

5.2.4.5 *Organic matter content*

Organic matter content was estimated by measuring loss on ignition. For each sample, 20 g of oven-dry soil was placed in a crucible and combusted at 650°C in a muffle furnace for two hours. Samples were cooled and then reweighed. Loss on ignition was calculated as the mass of oven-dry soil subtracted from the mass of ignited soil divided by the mass of oven-dry soil (multiplied by 100 %). It was expressed in 'g per 100g oven-dry soil'.

5.2.4.6 *Air and water-filled porosity*

The water-filled porosity was equal to the volumetric water content and so was expressed in 'cm³ H₂O cm⁻³ soil'. Air-filled porosity was estimated as the difference

between the water-filled porosity and the total pore volume, being expressed in 'cm³ air cm⁻³ soil'.

5.2.4.7 *pH*

An electrometric method using a millivoltmeter pH meter with a combination pH electrode was utilised to estimate surface and sub-surface soil pH. 10 g of fresh soil was added to 20 ml of distilled water and the suspension was shaken on a mechanical shaker for 20 minutes. The calibrated pH meter was then used to measure suspension pH.

A further minor investigation was carried out in spring in the heavily trampled and undisturbed surface soils of Tocil Wood. The determination of exchangeable calcium plus magnesium via titration and exchangeable hydrogen and magnesium was undertaken on samples according to the methods delineated by Rowell (1994).

5.2.4.8 *Estimations of visitor numbers*

Visitor counts for each wood were extrapolated from the data collected in Chapter 2. The three samples making up each sampling block were removed from trails that were nearby to pressure sensitive counter stations. Thus, approximations of the total number of visitors walking through sampling areas per year were possible. The average proportion of visitor numbers in each wear class was combined with the average visitor numbers to give an overall estimate of wear class use for any particular sampling block.

5.2.5 *Analysis of results*

5.2.5.1 *Data organisation*

Each soil parameter was examined to investigate any differences within and between study sites and seasons in wear class zones at the two soil depths. Seasonal variation was examined by dividing groups of sampling blocks from both woodland sites into

discrete seasonal categories depending on the time of sampling. The groups formulated irrespective of sampling year and were:

winter (December, January & February)

spring (March, April & May)

summer (June, July & August)

autumn (September, October & November)

Site data were combined and examined independently, erring any statistical comparison to caution.

5.2.5.2 *Statistical analysis*

Statistical analysis was performed using SYSTAT 5.2.1. Some data sets were transformed to conform to the assumptions of homoscedasticity and normality with regard to the values of the dependent variable (Zar 1984). Liliefors test ensured the normal distribution of samples.

5.3 Results

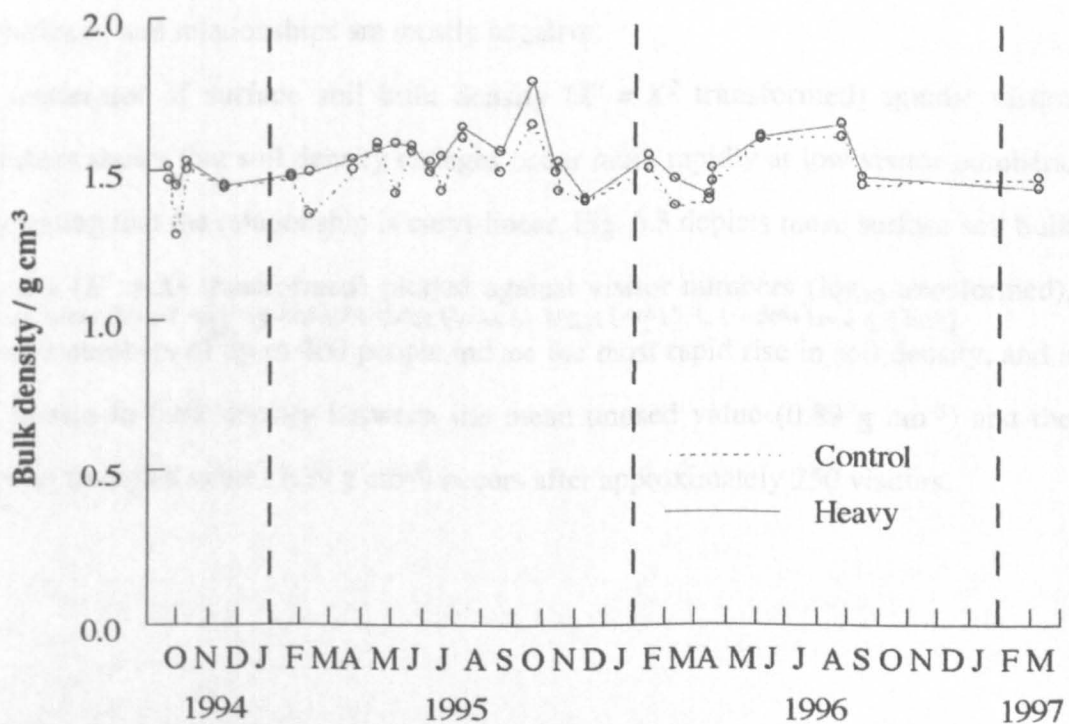
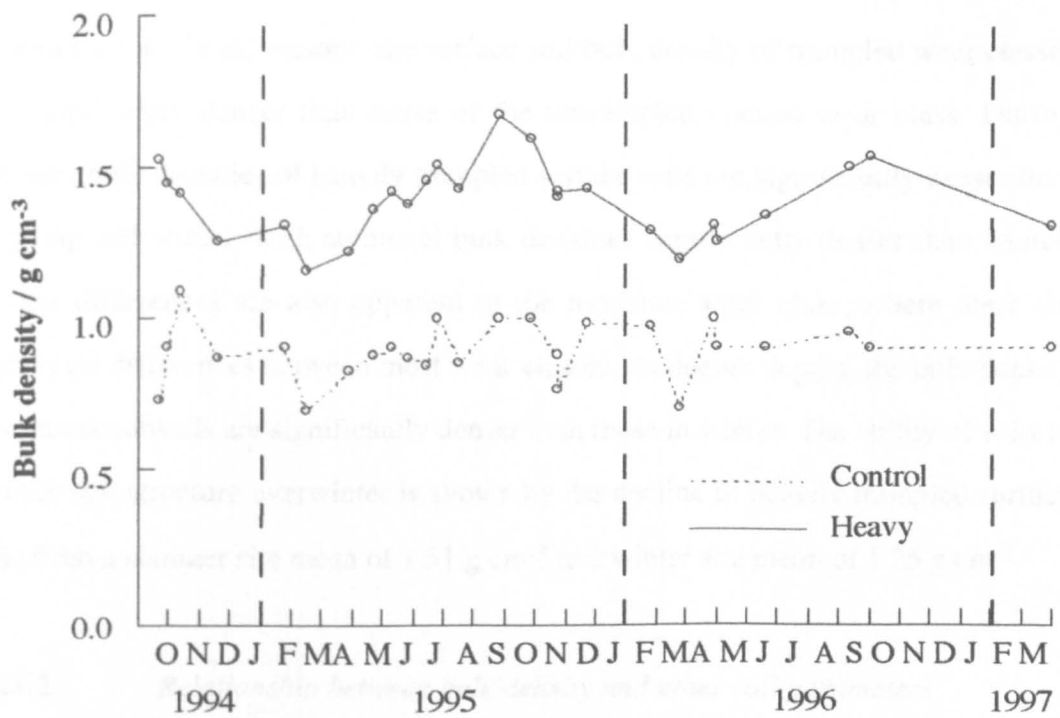
5.3.1 Bulk density

5.3.1.1 *Differences within and between seasons and sites*

Bulk densities of heavily trampled surface soils reach a summer maximum of 1.67 g cm^{-3} , before falling to a winter minimum of 1.15 g cm^{-3} . There is a summer maximum of 1.00 g cm^{-3} and a winter minimum of 0.71 g cm^{-3} in control surface soils. The rise in soil bulk density in trail centres by 0.50 g cm^{-3} means that heavily trampled soils increase by 56 % of the density of undisturbed soils. Such increases are most evident during summer (0.58 g cm^{-3}) and least in winter (0.41 g cm^{-3}). The seasonal fluctuations in soil bulk density are depicted as changes to sampling blocks in heavy and control wear class zones in all three sites for surface soils (Fig. 5.1) and sub-surface soils (Fig. 5.2) over cumulative time. Peak levels of compaction occur in the centre of trails where the most use is concentrated. Variation in the density of surface soils along trampled trails shows the greatest seasonal flux, and even at the sub-surface level marked differences are evident.

The bulk densities at surface and subsoil depths are significantly higher in trampled areas than the untrampled control areas (Appendices 5.1, 5.2, 5.3 & 5.4). Indeed, surface soil bulk densities of heavily and moderately trampled zones are significantly denser than the light and control wear classes in all three sites, and subsoil bulk density differences between wear classes are significant only in Tocil Wood and as a site mean. Overall bulk densities are significantly higher in subsoils compared to surface soils, with a striking difference of 0.58 g cm^{-3} between the two soil depths in the control wear class ($t = 37.6$, $df = 77$, $p < 0.001$). There is also a significant difference of 0.14 g cm^{-3} between the two soil depths in the heavily trampled wear class ($t = 9.2$, $df = 77$, $p < 0.001$).

Surface soil bulk density comparisons between wear classes in all four seasons also differ significantly (Appendix 5.2), whilst those for sub-surface soils do not



(Appendix 5.4). In all seasons, the surface soil bulk density of trampled wear classes are significantly denser than those of the untrampled control wear class. During summer, bulk densities of heavily trampled surface soils are significantly denser than in spring and winter, with autumnal bulk densities significantly denser than winter. Similar differences are also apparent in the moderate wear class, where there are significant differences between most wear classes. At deeper depths, the bulk density of summer subsoils are significantly denser than those in winter. The ability of soils to recover soil structure overwinter is shown by the decline in heavily trampled surface soils from a summer site mean of 1.51 g cm^{-3} to a winter site mean of 1.25 g cm^{-3} .

5.3.1.2 *Relationship between bulk density and other soil parameters*

There is a highly significant positive correlation between visitor numbers and surface soil bulk density (Table 5.1). In addition, the trend of a summer maximum and a winter minimum is strongly related to the seasonal visitor use patterns. The sub-surface soils also yield a significant positive correlation with visitor numbers ($r_s = 0.259$, $n = 104$, $p < 0.01$). Correlations with all other surface soil variables are significant, and relationships are mostly negative.

A scatterplot of surface soil bulk density ($X' = X^2$ transformed) against visitor numbers shows that soil density changes occur more rapidly at low visitor numbers, suggesting that the relationship is curvi-linear. Fig. 5.3 depicts mean surface soil bulk density ($X' = X^2$ transformed) plotted against visitor numbers (\log_{10} transformed).
 → Shows wear classes aggregated into three blocks of H & H (right), L (middle) and C (left)
 Visitor numbers of up to 400 people induce the most rapid rise in soil density, and a 50 % rise in bulk density between the mean unused value (0.89 g cm^{-3}) and the highest trampled value (1.39 g cm^{-3}) occurs after approximately 250 visitors.

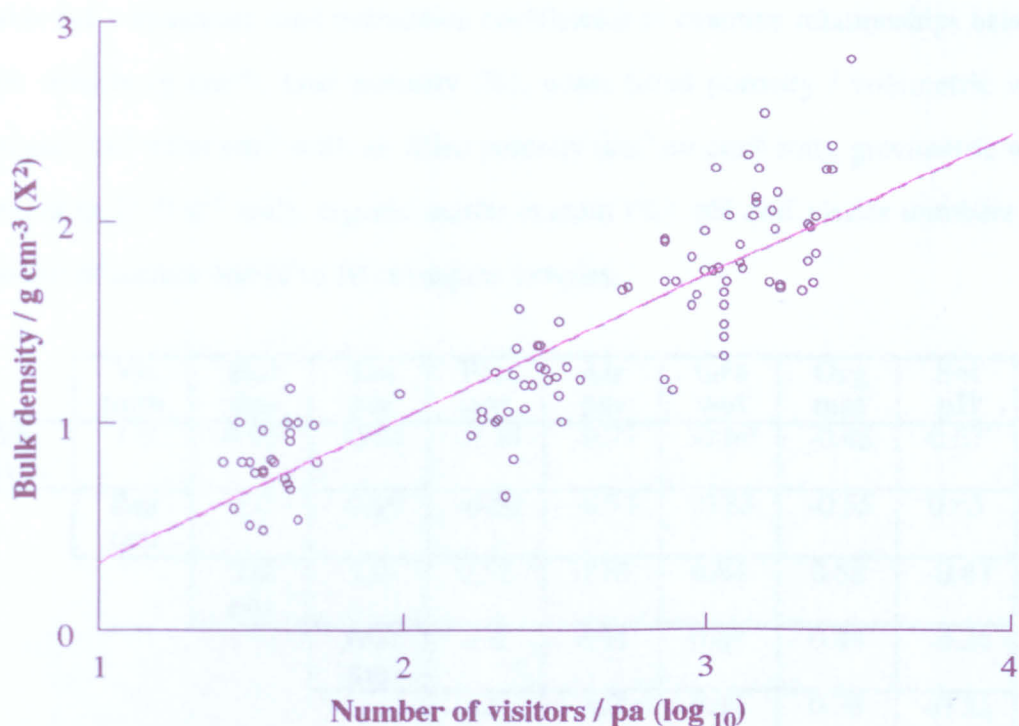


Fig. 5.3 - The relationship of number of visitors per year (\log_{10}) regressed against surface soil bulk density (X^2) (X^2 $y = -0.374 + 0.702 (\log_{10}) x$; $r^2 = 0.783$, $F = 368.9$, $p < 0.001$).

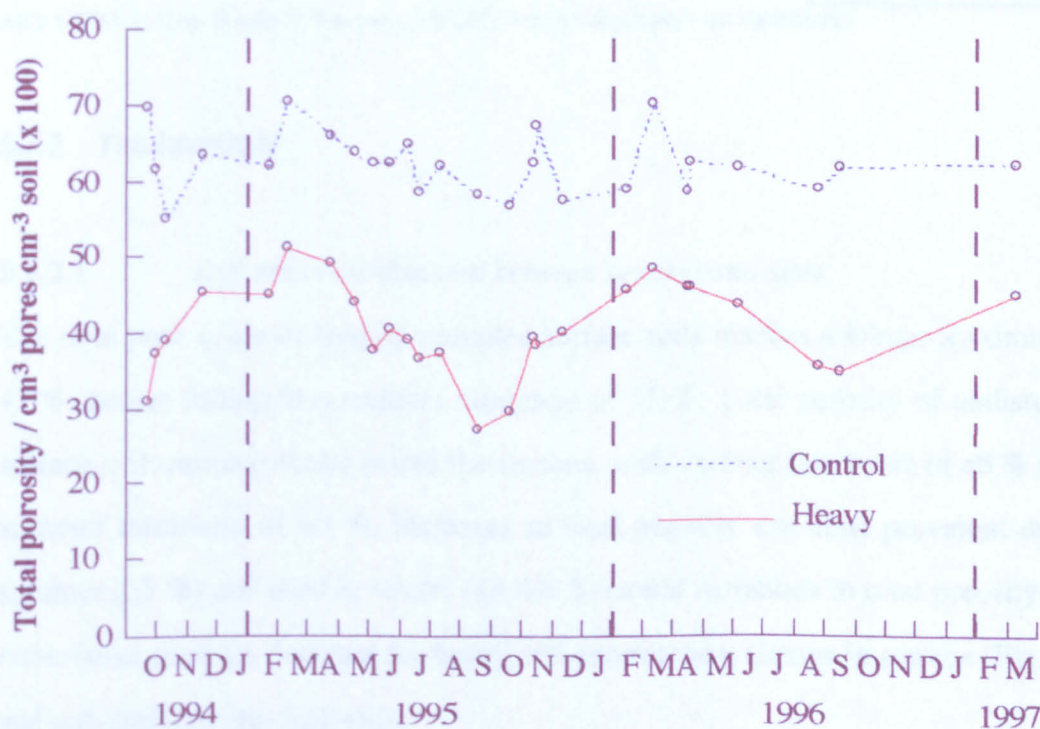


Fig. 5.4 - Periodic measurements of surface soil total porosity (0 - 10 cm depth) in heavily trampled and undisturbed control areas of three woodland sites, 1994 to 1997.

Table 5.1 - Spearman rank correlation coefficients to examine relationships between bulk density (g cm^{-3}), total porosity (%), water filled porosity / volumetric water content ($\text{cm}^3 \text{ water cm}^{-3} \text{ soil}$), air filled porosity ($\text{cm}^3 \text{ air cm}^{-3} \text{ soil}$), gravimetric water content ($\text{g H}_2\text{O g}^{-1} \text{ soil}$), organic matter content (%), pH and visitor numbers (per annum) of surface soil (0 to 10 cm depth) samples.

	Vis num	Bul den	Tot por	Wat por	Air por	Gra wat	Org mat	Soi pH
Vis Num	1.0	0.90	-0.89	-0.34	-0.77	-0.69	-0.45	0.67
Bul den		1.0	-0.99	-0.50	-0.75	-0.83	-0.55	0.65
Tot por			1.0	0.52	0.75	0.84	0.58	-0.63
Wat por				1.0	0.33	0.87	0.33	-0.24
Air por					1.0	0.33	0.38	-0.55
Gra wat						1.0	0.49	-0.47
Org mat							1.0	-0.38
Soi pH								1.0

All $p \leq 0.001$ (except Soi pH & Wat por - $p \leq 0.05$; Wat por & Air por - not significant)

5.3.2 Total porosity

5.3.2.1 Differences within and between seasons and sites

The total pore space of heavily trampled surface soils reaches a winter maximum of 47 %, before falling to a summer minimum of 35 %. Total porosity of undisturbed surface soils remains stable across the seasons, with a winter maximum of 65 % and a summer minimum of 60 %. Increases in total porosity are most prevalent during summer (25 %) and least in winter (18 %). Seasonal variations in total porosity over cumulative time are depicted for heavy and control wear classes in surface (Fig. 5.4) and sub-surface (Fig. 5.5) soils.

The total porosity/s of surface and sub-surface soils peak in undisturbed zones and decline with increasing trampling intensity (Appendices 5.1, 5.2, 5.3 & 5.4).

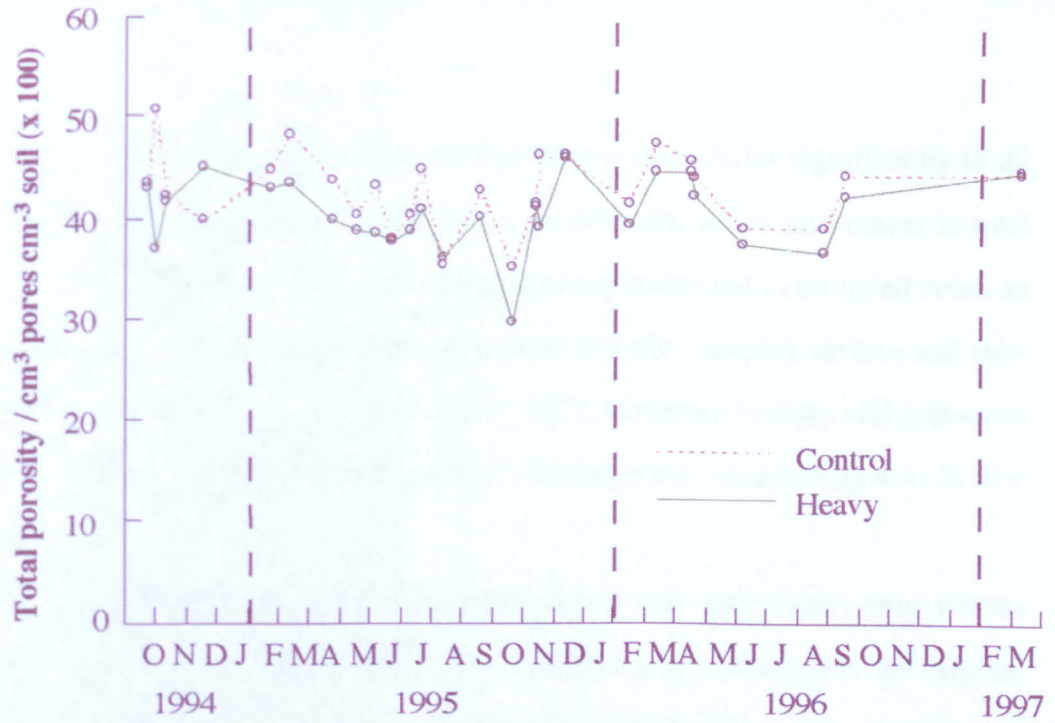


Fig. 5.5 - Periodic measurements of sub-surface soil total porosity (10 - 30 cm depth) in heavily trampled and undisturbed control areas of three woodland sites, 1994 to 1997.

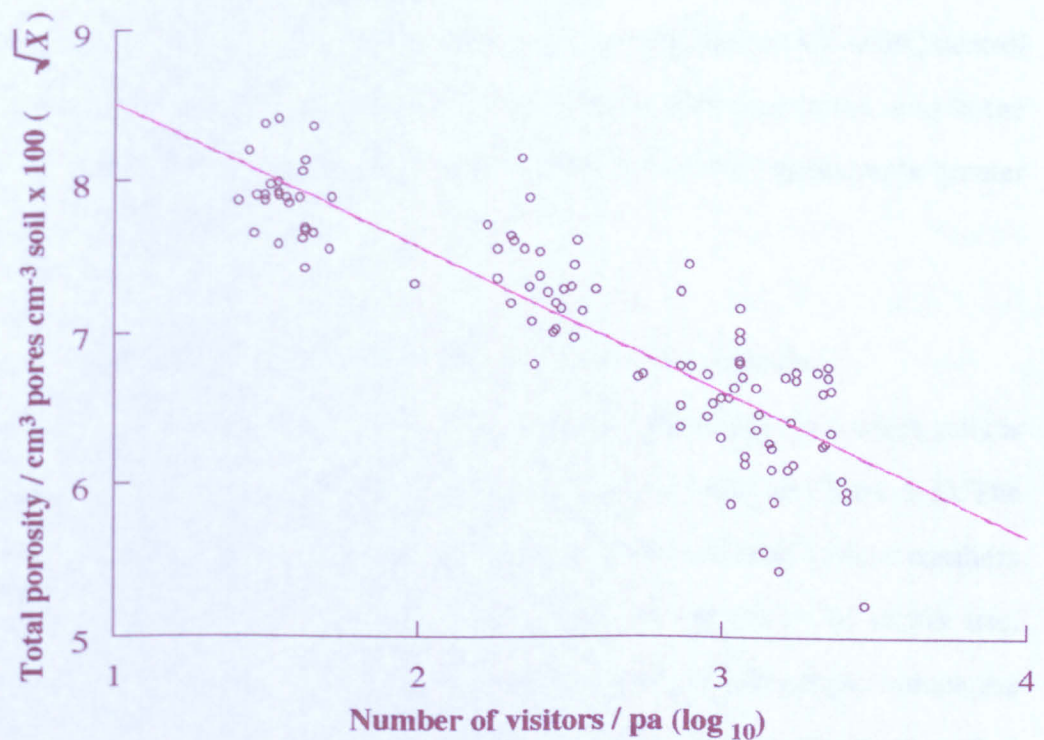


Fig. 5.6 - The relationship of number of visitors per year (\log_{10}) with surface soil total porosity (\sqrt{X}) ($(\sqrt{X}) y = 9.446 - 0.944 (\log_{10}) x$; $r^2 = 0.765$, $F = 332.7$, $p < 0.001$).

Accordingly, surface soil differences between wear classes differ significantly in all cases. The impact of trampling extends to deeper subsoils, where differences in total porosity are significantly greater in untrampled zones compared to trampled zones in Tocil Wood and as a site mean. Pore volumes of heavily trampled surface and sub-surface soils are similar ($t = 0.6$, $df = 77$, $p = 0.57$). However, surface soil porosities of control zones are significantly higher by 22 % compared to subsoils ($t = 30.3$, $df = 77$, $p < 0.001$).

In all seasons, control and lightly trampled surface soils are significantly more porous than moderately and heavily trampled soils, increasing by a third over the original undisturbed porosity (Appendix 5.2). In heavily trampled trail centres, surface soil porosity's during winter and spring are significantly greater than those in summer and autumn. Even the porosity's of lightly trampled trail margins during winter are significantly more porous than in summer, so the magnitude of differences lessens with declining trampling intensity. Subsoil porosity's of heavy, moderate and control wear classes during winter are also significantly greater than in summer, and in the light wear class both winter and autumn subsoil porosity's are significantly greater than summer (Appendix 5.4).

5.3.2.2 *Relationship between total porosity and soil parameters*

The negative correlation between visitor numbers and total porosity in surface soils is highly significant, as are the correlations with all other soil variables (Table 5.1). The regression plot of mean total porosity (\sqrt{X} transformed) against visitor numbers (\log_{10} transformed) (Fig. 5.6) is highly significant. At low levels of visitor use, eradication of pore space is rapid. Visitor numbers of up to 400 people induce the most concentrated loss, with a 50 % drop in total porosity between the mean unused value (62.1 %) and the lowest trampled value (40.3 %) caused by approximately 305 visitors.

5.3.2.3 *Proportional changes in soil constituents*

To illustrate the proportional changes in soil constituents that are modified by trampling, surface soil volumes occupied by soil material, water filled porosity and air filled porosity are illustrated graphically for all wear class zones in Tocil Wood (Fig. 5.7), Tilehill Wood (Fig. 5.8) and Crackley Wood (Fig. 5.9).

5.3.3 *Water filled porosity (volumetric water content)*

5.3.3.1 *Differences within and between seasons and sites*

Water filled porosity's of heavy and control wear class surface soils plotted against cumulative time (Fig. 5.10) show a summer minimum in trail centres of $0.24 \text{ cm}^3 \text{ H}_2\text{O cm}^{-3} \text{ soil}$ and a winter maximum of $0.54 \text{ cm}^3 \text{ H}_2\text{O cm}^{-3} \text{ soil}$. However, surface and subsoil water filled porosity's in the three sites are generally similar across the range of wear classes (Appendices 5.1, 5.2, 5.3, 5.3), with few significant differences between wear classes in any of the sites. The water filled porosity is significantly greater in heavily trampled and control surface soils compared to subsoils ($t = 3.8$, $df = 25$, $p < 0.001$ and $t = 5.7$, $df = 25$, $p < 0.001$ respectively).

In winter, autumn and spring, water filled porosity's are slightly lower in trampled wear classes compared to control zones, but not significantly so except during autumn (Appendix 5.2). Trends are reversed during summer, where trampled wear classes are proportionally wetter than undisturbed off-trail soils, but not significantly so. The water filled porosity's of heavily trampled surface soils in winter are significantly wetter than in autumn and summer, and winter and autumn water filled porosity's of lightly trampled soils are significantly wetter than those in summer. In control soils, the water filled porosity's in winter are significantly greater than those in autumn and spring, and all are greater than the dry soils of summer.

5.3.3.2 *Relationship between water filled porosity and soil parameters*

The negative correlation between water filled porosity and visitors numbers is significant in surface soils, whilst nearly all correlations with other soil variables are

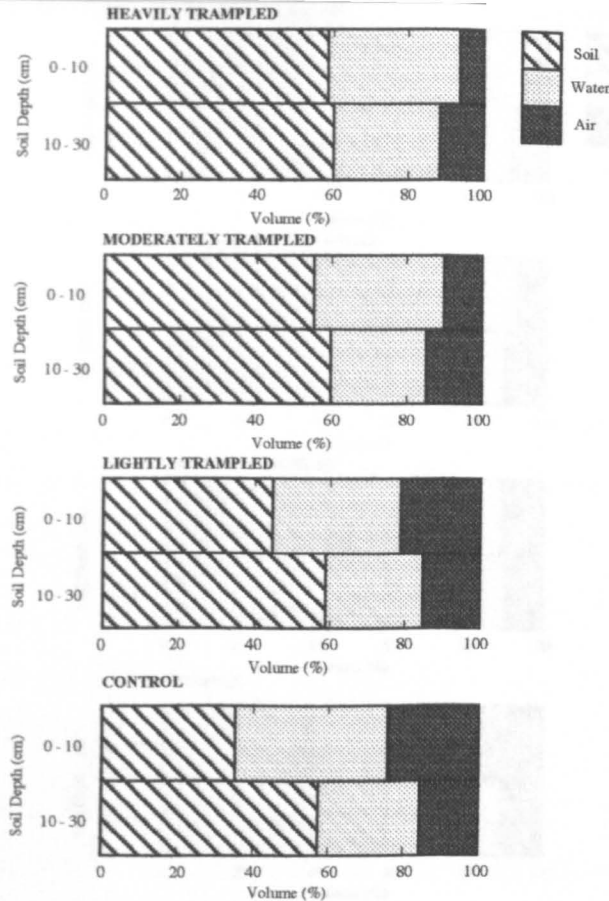


Fig. 5.7 - Volume relationship of soil material, water and air in heavy, moderate light and control wear class zones in Tocil Wood, as a total average from 1994 to 1996.

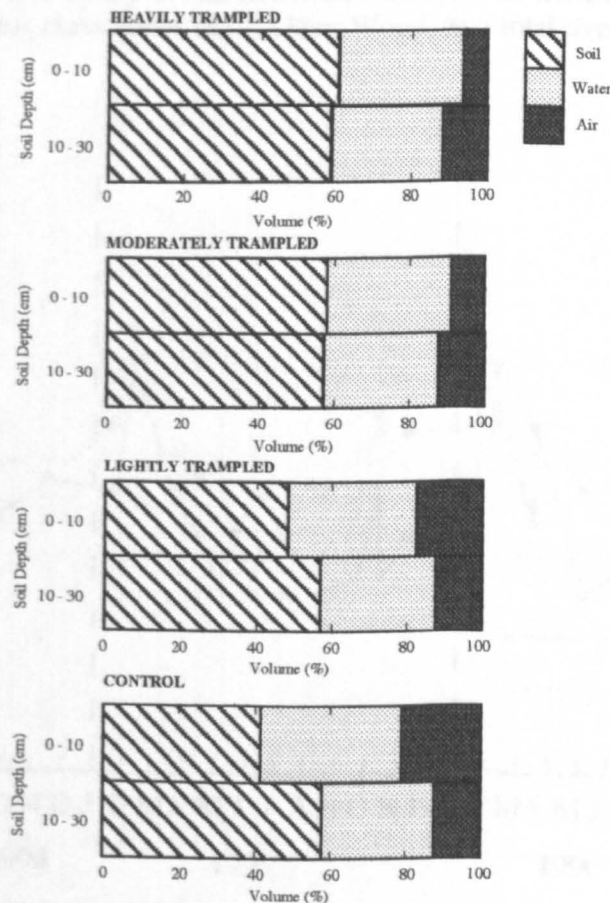


Fig. 5.8 - Volume relationship of soil material, water and air in heavy, moderate light and control wear class zones in Tilehill Wood, as a total average from 1994 to 1996.

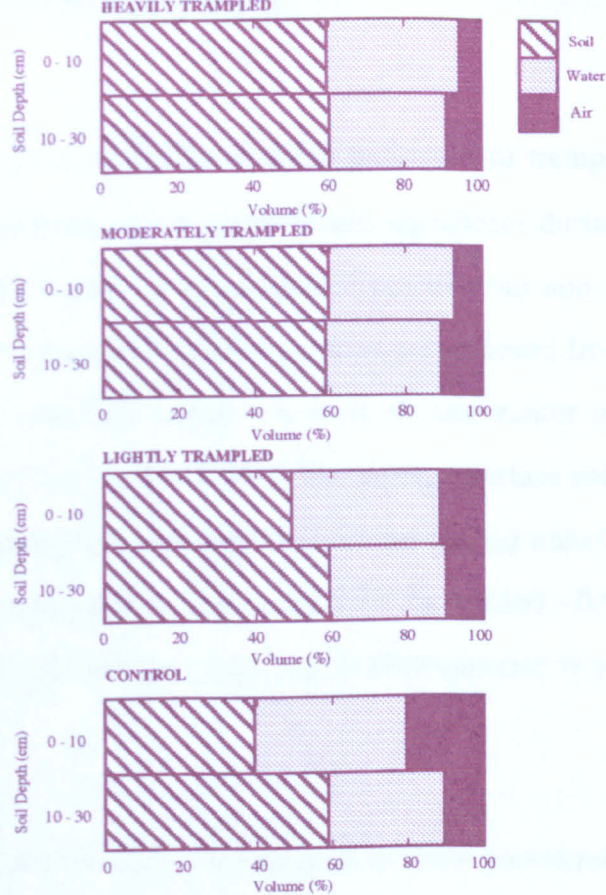


Fig. 5.9 - Volume relationship of soil material, water and air in heavy, moderate light and control wear class zones in Crackley Wood, as a total average from 1995 to 1997.

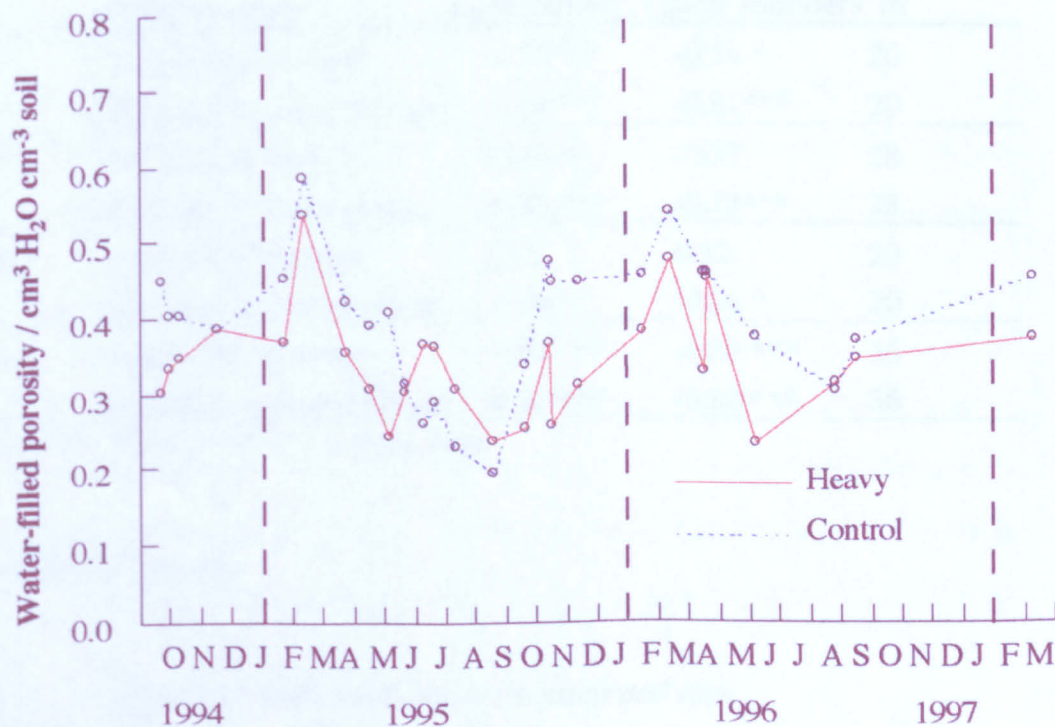


Fig. 5.10 - Periodic measurements of surface soil water-filled porosity (0 - 10 cm depth) in heavily trampled and unused control areas of three woodland sites, 1994 to 1997.

also significant (Table 5.1). Correlations with the indicators of trampling intensity (visitor numbers and bulk density) are negative and significant during winter and autumn, negative but non-significant in spring and positive but non-significant in summer (Table 5.2). When the summer survey results are removed from the overall comparison, correlations with bulk density ($r_s = -0.69$) and visitor numbers ($r_s = -0.49$) are also significant ($n = 84$, $p < 0.001$). The average surface soil water filled porosity value for each sampling block regressed against (\log_{10}) transformed visitor numbers shows that the relationship is significant ($((\sqrt{X}) y = 0.667 - 0.028 (\log_{10}) x$; $F = 10.6$, $df = 103$, $p < 0.001$) but the coefficient of determination is very low ($r^2 = 0.095$).

Table 5.2 - Spearman rank correlation coefficients to show paired relationships of surface soil (0 to 10 cm depth) water filled porosity ($\text{cm}^3 \text{H}_2\text{O cm}^{-3} \text{soil}$) and gravimetric water content ($\text{g H}_2\text{O g}^{-1} \text{soil}$) with bulk density (g cm^{-3}) and visitor numbers during each season.

Season	Water content	Bulk density	Visitor numbers	df
Winter	Water filled porosity	-0.75 ***	-0.54 *	20
	Gravimetric water content	-0.94 ***	-0.81***	20
Spring	Water filled porosity	-0.53 **	-0.37	28
	Gravimetric water content	-0.86 ***	-0.73***	28
Summer	Water filled porosity	0.33	0.32	20
	Gravimetric water content	-0.56 *	-0.54 *	20
Autumn	Water filled porosity	-0.84 ***	-0.66 ***	36
	Gravimetric water content	-0.90 ***	-0.86 ***	36

* - * sig. at $p \leq 0.05$; ** sig. at $p \leq 0.01$; *** sig. at $p \leq 0.001$

5.3.4 Air filled porosity

5.3.4.1 Differences within and between seasons and sites

Heavy trampling severely reduces the air-filled pore space of surface soils, with a summer minimum of $0.03 \text{ cm}^3 \text{air cm}^{-3} \text{soil}$ rising twelvefold to $0.35 \text{ cm}^3 \text{air cm}^{-3} \text{soil}$

in control soils. The seasonal variation in air filled porosity is illustrated in heavy and control surface soils against cumulative time (Fig. 5.11). The air filled porosity of heavily compacted soils during summer occasionally drops to zero, suggesting that the obliteration of air-filled pores by trampling is strongly related to seasonal visitor use densities.

The air filled pore spaces of surface soils are higher in undisturbed areas than along trampled trails, but similar in subsoils (Appendices 5.1, 5.2, 5.3 & 5.4). As a site mean, the air filled porosity of trail centre surface soils are a quarter of those off-trail. The proportion of soil air in undisturbed and lightly trampled soils is significantly greater than that found in moderately and heavily trampled zones. The air filled porosity's of heavily trampled subsoils are almost double those of surface soils, with a significant difference of $0.05 \text{ cm}^3 \text{ air cm}^{-3} \text{ soil}$ ($t = 4.5$, $df = 25$, $p < 0.001$). The opposite trend occurs in untrampled zones, where surface soil air filled porosity are a factor of 1.6 greater than subsoils, with a significant difference of $0.08 \text{ cm}^3 \text{ air cm}^{-3} \text{ soil}$ ($t = 3.9$, $df = 25$, $p < 0.001$).

During winter and spring, the air filled porosity's of untrampled and lightly trampled zones are significantly higher than moderately and heavily trampled trail centres (Appendix 5.2). In heavily trampled surface soils, the air filled porosity of spring is significantly higher than in summer. Additionally, along lightly trampled trail margins and undisturbed zones, the air-filled pore space during summer is significantly lower than most of the other seasons.

5.3.4.2 *Relationship between air filled porosity and soil parameters*

The negative correlation between surface soil air filled porosity and visitor numbers is highly significant, with additional highly significant negative correlations with bulk density and pH (Table 5.1). There are significant positive correlations with total porosity, organic matter and gravimetric water content.

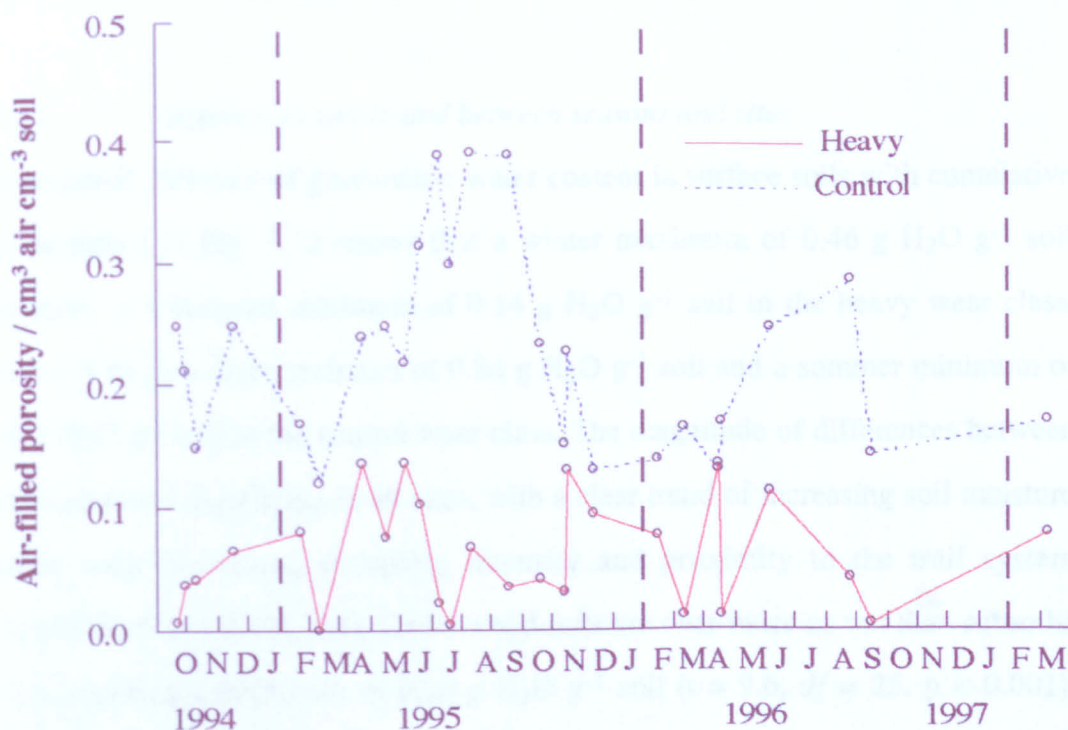


Fig. 5.11 - Periodic measurements of surface soil air-filled porosity (0 - 10 cm depth) in heavily trampled and undisturbed control areas in three woodland sites, 1994 to 1997.

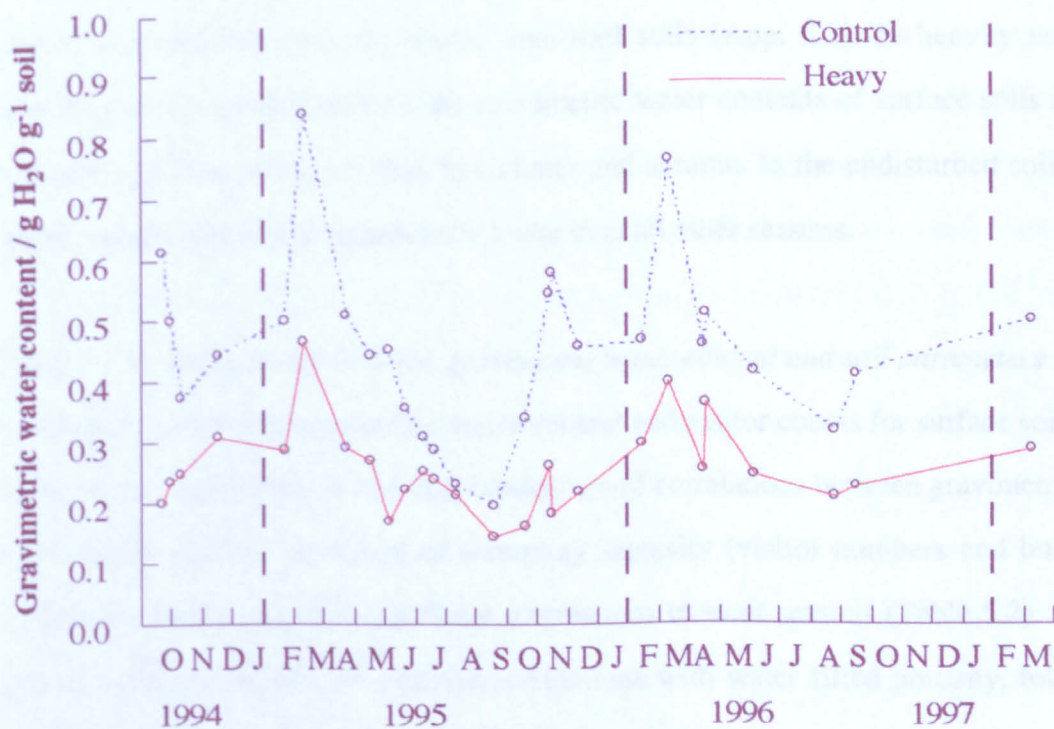


Fig. 5.12 - Periodic measurements of surface soil gravimetric water content (0 - 10 cm depth) in heavily trampled and undisturbed areas of three woodland sites, 1994 to 1997.

5.3.5 Gravimetric water content

5.3.5.1 *Differences within and between seasons and sites*

The seasonal variation of gravimetric water content in surface soils with cumulative time depicted in Fig. 5.12 shows that a winter maximum of $0.46 \text{ g H}_2\text{O g}^{-1} \text{ soil}$ plummets to a summer minimum of $0.14 \text{ g H}_2\text{O g}^{-1} \text{ soil}$ in the heavy wear class. There is a high winter maximum of $0.84 \text{ g H}_2\text{O g}^{-1} \text{ soil}$ and a summer minimum of $0.19 \text{ g H}_2\text{O g}^{-1} \text{ soil}$ in the control wear class. The magnitude of differences between wear classes are significant in all sites, with a clear trend of increasing soil moisture content with decreasing trampling intensity and proximity to the trail system (Appendices 5.1, 5.2, 5.3, 5.4). Undisturbed soils are over twice as wet ^{as} ~~than~~ subsoils, with a significant difference of $0.26 \text{ g H}_2\text{O g}^{-1} \text{ soil}$ ($t = 9.6$, $df = 25$, $p < 0.001$). Heavily trampled surface soils are marginally wetter by $0.059 \text{ g H}_2\text{O g}^{-1} \text{ soil}$ than subsoils ($t = 4.5$, $df = 25$, $p < 0.001$).

Gravimetric water contents of surface soils differ significantly in winter, spring and autumn, with off-trail soils far wetter than trail soils (App. 5.2). In heavily and moderately trampled trail centres, the gravimetric water contents of surface soils in winter are significantly higher than in summer and autumn. In the undisturbed soils, summer water contents are significantly lower than all other seasons.

5.3.5.2 *Relationship between gravimetric water content and soil parameters*

The correlation between gravimetric water content and visitor counts for surface soils is negative and significant. A seasonal breakdown of correlations between gravimetric water content and the indicators of trampling intensity (visitor numbers and bulk density) also yields negative significant correlations in most seasons (Table 5.2). In addition, there are significant positive correlations with water filled porosity, total porosity, organic matter content and air filled porosity, and a significant negative correlation with soil pH (Table 5.1). Gravimetric water content values (\log_{10} transformed) regressed with (\log_{10}) transformed visitor numbers gives a relationship

which is significant ($((\log_{10}) y = -0.109 - 0.159 (\log_{10}) x$; $F = 84.2$, $df = 103$, $p < 0.001$), with a low coefficient of determination ($r^2 = 0.43$).

5.3.6 Organic matter content

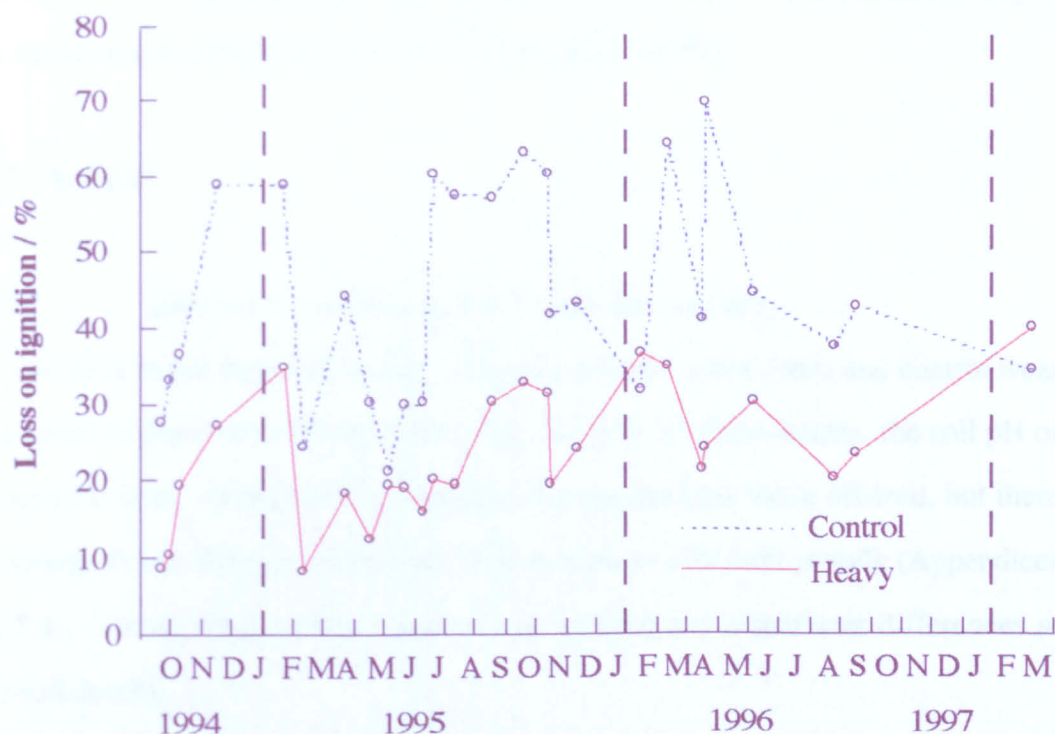
5.3.6.1 Differences within and between seasons and sites

The organic matter content of heavily trampled and control untrampled surface soils plotted against cumulative time (Fig. 5.13) shows a summer minimum of 8 % and spring maximum of 64 % in the two wear classes respectively. The organic matter content of undisturbed surface soils are higher than those of trampled soils, but remain similar across the range of wear classes in subsoils (Appendices 5.1, 5.2, 5.3 & 5.3). Undisturbed soils are significantly richer in organic matter content than the moderately and heavily trampled soils of trail centres. Indeed, as a site mean off-trail soils are up to twice as rich in organic matter than trail centre soils. The concentration of organic matter in surface heavily trampled soils means that the difference of 18 % compared to subsoils is significant ($t = 5.4$, $df = 15$, $p < 0.001$), with a highly significant difference of 38 % in the control wear class ($t = 5.7$, $df = 15$, $p < 0.001$).

The seasonal differences between wear classes are all significant in surface soils (Appendix 5.2), but not in subsoils (Appendix 5.4). Additionally, the organic matter of lightly trampled and control surface soils during winter are significantly richer than in autumn. The depletion in organic matter content along trail centres is such that seasons do not differ statistically in terms of organic matter content.

5.3.6.2 Relationship between organic matter content and soil parameters

The correlation between organic matter content and visitor numbers is significant, as are relationships with all other soil variables (Table 5.1). The organic matter content (\sqrt{X} transformed) regressed against visitor numbers (\log_{10} transformed) depicts a significant relationship ($((\sqrt{X}) y = 7.939 - 0.983 (\log_{10}) x$; $F = 41.4$, $df = 103$, $p < 0.001$) with a low coefficient of determination ($r^2 = 0.289$). The correlation between



bulk density and organic matter combined for both soil depths for unused soils only is also negative and significant ($r_s = -0.651$, $n = 42$, $p < 0.001$).

5.3.7 Soil pH

5.3.7.1 *Differences within and between seasons and sites*

The variation in pH over cumulative time in heavy wear class zones and control wear class zones is depicted for surface soils (Fig. 5.14). In all four seasons, the soil pH of the heaviest worn surface soils are significantly greater than those off-trail, but there are no significant differences between wear classes in sub-surface soils (Appendices 5.2, 5.4). Comparisons between seasons fail to yield any significant differences at both soil depths.

Surface and subsoil pH are greatest in trampled wear classes compared to the untrampled wear class (Appendices 5.1, 5.2, 5.3 & 5.4). In most cases, the surface soil pH of heavy and moderate wear classes are significantly higher than those in light and control wear classes. The soil pH of heavily trampled surface soils are significantly higher than subsoils ($t = 5.0$, $df = 20$, $p < 0.001$), suggesting that trampled subsoils are more acidic. This contrasts with a marginally higher soil pH of control surface soils compared to subsoils ($t = 1.5$, $df = 20$, $p = 0.139$), suggesting that pH is similar throughout the soil profile.

5.3.7.2 *Relationship between pH and soil parameters*

There are significant positive correlations between soil pH and visitor numbers and bulk density, with all other correlations negative and significant (Table 5.1). Mean pH values regressed against visitor numbers (\log_{10} transformed) gave a significant relationship (Fig. 5.15).

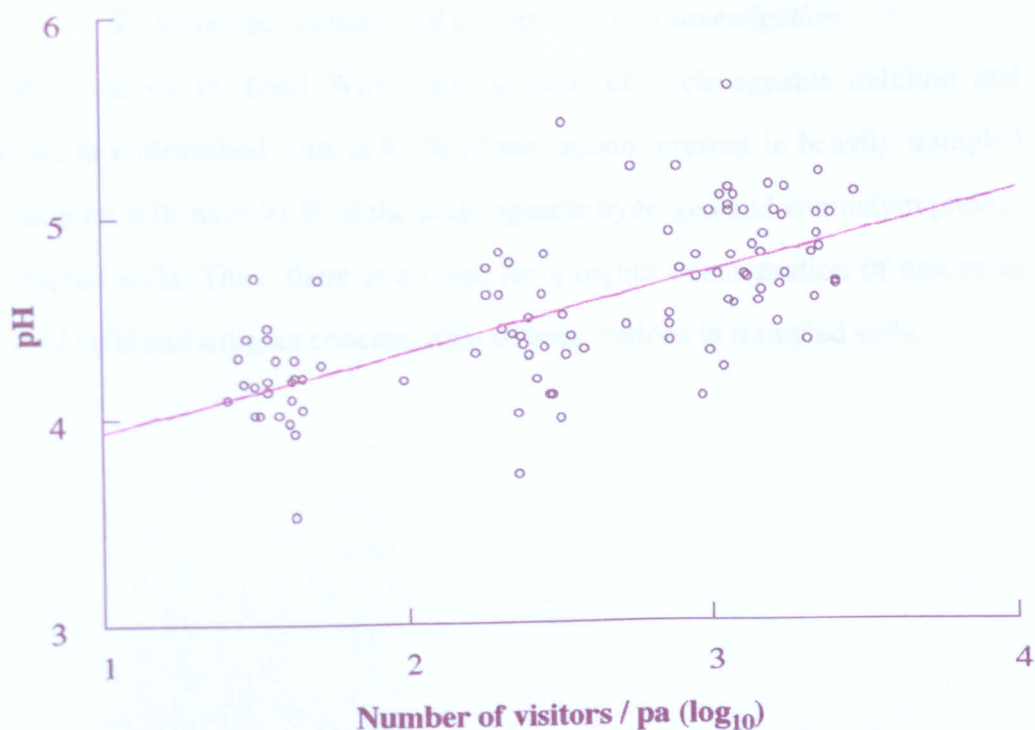


Fig. 5.15 - The effect of number of visitors per year (Log₁₀) on surface soil pH ($y = 3.547 + 0.391 \times (\text{Log}_{10})$; $r^2 = 0.433$, $F = 78.0$, $p < 0.001$).

5.3.7.3 *Exchangeable cations and anions - a minor investigation*

In a spring survey in Tocil Wood, the amount of exchangeable calcium and magnesium in undisturbed soils is 81 % of the amount present in heavily trampled soils. Trampled soils have 91 % of the exchangeable hydrogen and aluminium present in undisturbed soils. Thus, there is a trend for a higher concentration of anions in undisturbed soils and a higher concentration of basic cations in trampled soils.

Chapter 6

**THE IMPACT OF RECREATIONAL TRAMPLING ON WOODLAND SOIL
AND LITTER INHABITING MESOFAUNA AND MICRO-ORGANISMS**

6.1 Introduction

It is surprising that although ^{most} every kind of touristic impact on the natural landscape has a negative effect on the soil fauna, scant attention has been paid to the impact of recreational trampling on soil invertebrates (Anderson & Radford 1992, Meyer 1993, Speight 1973). The primary purpose of this chapter is to elucidate a more accurate assessment of the extent, severity and significance of trampling on woodland soil and litter invertebrate taxa and soil micro-organisms. The overall effects of recreational trampling on invertebrates living within the soil are poorly understood (Anderson & Radford 1992).

The extent of environmental degradation is assessed by examining changes in soil and litter dwelling invertebrate diversity, richness and abundance. As invertebrates are increasingly being perceived as viable indicators of levels of disturbance in ecosystems, emphasis is placed on the generation of a reliable biological indicator for soil compaction.

6.1.1 Research proposals

- To estimate the seasonal fluctuations in population density (m^{-2}) of woodland surface soil and litter mesofauna in heavily trampled path centres, lightly trampled path margins and undisturbed control zones.
- To quantify the relationship between mesofauna abundance with indicators of trampling intensity, litter type and other physical and chemical soil parameters divulged from Chapter 5.
- To generate a simple biological indicator for soil compaction using Acari body size. Acari are utilised because they are generally the most abundant arthropod group in litter and soil (Murphy 1962, Tilling 1987), and show size variability with fluctuations in pore size (Ingellog *et al.* 1977).
- To monitor changes in the seasonal in-situ response of micro-organism biomass and respiration rates in trampled and adjacent undisturbed surface and sub-surface woodland soils in an effort to clarify the effects of trampling on

biological processes in the soil. Such concepts are only partly understood (Whalley *et al.* 1995).

- To suggest priorities for the management of woodland invertebrates for conservation in recreational sites. Soil horizons and the soil rhizosphere constitute a huge reservoir for biodiversity (Andre *et al.* 1994), so there is an acknowledged basis for soil fauna conservation.

6.2 Materials and methods

Throughout this study, the term 'soil fauna' is used to refer to all forms of animal life which inhabit woodland soil or litter for part or all of their life-cycles. Soil mesofauna (0.1 to 1.0 mm) includes Enchytraeidae, Arachnida and the smaller Insecta which move around in soil cavities, and the mainly burrowing macrofauna (> 5 mm) include large arthropods, Mollusca and Lumbricidae (Murphy 1962). In the context of this study, mesofauna includes smaller macrofauna taxa. The microbial biomass is defined as the mass of living micro-organisms in the soil, and includes microscopic unicellular bacteria and filamentous fungi (Rowell 1994).

The soils of Tocil Wood, used for the microbial and mesofauna experiments, are dominated by mull litter types (Bradley pers. commn. 1997). The soils of Tilehill Wood, used for the macro- and mesofauna sampling only, are dominated by mor and transitional moder litter types (Beard 1979).

6.2.1 Macro- and meso-fauna

Procedures for extracting soil and litter macro- and meso-fauna follow methodology outlined by Jackson & Raw (1973) and MacFayden (1962). A dry Tullgren funnel technique was used to extract fauna from soil and litter samples. The dry funnel extraction technique caught small, relatively immobile species that inhabit soil macropores, which are tolerant of water loss and are capable of rapid responses to immediate environmental fluctuations in temperature and moisture levels (Jackson & Raw 1973, Purvis & Curry 1980, Slingsby & Cooke 1992).

6.2.1.1 Field sampling

Fieldwork sites were sampled six times in Tocil Wood and four times in Tilehill Woods at irregular time intervals between late 1995 and early 1997. Samples were removed from heavily compacted trail centres, trail margins and undisturbed zones. In each zone, mean leaf litter depth was estimated by measuring litter depth at each corner of a randomly placed 0.1 m² quadrat. A quantity of 0.1 m² of surface leaf litter

was removed from each quadrat and placed in a plastic bag. Single surface soil cores were then extracted from the exposed soil surface by utilising a portable root auger measuring 10 cm in diameter and 5 cm in depth. The auger was sunk to the 5 cm level and rotated about its vertical axis to loosen the core. The size of the auger was in accordance with MacFayden's (1962) suggestion that 10 cm² would yield high enough numbers for arthropod community studies.

6.2.1.2 *Extraction and identification of soil and litter organisms*

Samples were hand-sorted to remove larger invertebrates. A number of Tullgren funnels were constructed, consisting of bottomless black 15 cm diameter plant pots, with convex aluminium gauzes of 5 mm mesh diameter attached to their bases. Soil cores and litter samples were added to separate pots clamped into large plastic funnels, and were suspended beneath 25 watt lamps for four days. Samples were hand mixed at 24 hour intervals so as to maximise extraction efficiency. The humidity gradient enforced by increased light, heat and dry conditions from the lamp was sufficient to force soil fauna from the soil and litter samples through the gauze and into a collection vessel containing 80 % alcohol located below the funnel. This downward migration occurs because soil fauna shows a natural aversion to light and hot, dry conditions (Slingsby & Cooke 1992). After extraction, each catch was transferred to a petri-dish for subsequent identification.

Petri-dishes containing catches were placed over a predrawn circumference of the dish on graph paper divided into 5 mm squares. Excess fluid was removed from petri-dishes and observations commenced from the centre of the dish outwards, using a dissection microscope. Monitoring proceeded through each 5 mm square so that all organisms in every square were identified and counted. The volume of each soil core when combined with the volume of leaf litter for each sample unit derived the population density of organisms (per cm⁻³ and extrapolated to per m⁻²). The grid size scale also enabled Acari body length to be estimated, with three main size categories

of large (> 5 m long), moderate (between 0.2 and 0.5 mm in length) and small size (< 0.2 mm long).

Soil organisms were identified to the Order level using the keys by Kevan (1962) and Tilling (1987). Direct comparisons of soil fauna abundance were made with soil physical and chemical measurements of Chapter 5, and visitor counts from Chapter 2. Samples were purposely removed from trails that were located nearby to pressure sensitive counter stations and soil sampling blocks.

6.2.2 *Determination of microbial biomass by a fumigation-extraction method*

6.2.2.1 *Sampling in the field*

Two permanent 1 x 3 m² quadrats were set up either running parallel to the line of wear in the centre of a heavily used footpath and in adjacent undisturbed ground in Tocil Wood. A direct comparison of this nature assumes that soils are at equilibrium with the presence or absence of trampling pressure, and that any differences can be mainly attributed to the impact of physical disturbance.

Three soil samples were collected at five time intervals during 1995 from separate 0.1 m² sub-plots located within the permanent quadrat. Single soil cores were excavated from surface sub-plots after the upper layers of litter had been removed to expose the humus layer. A 10 cm diameter and 10 cm depth root auger was used to extract samples. An auger of this size was deemed suitable because in most natural soils, the majority of micro-organisms live in the uppermost few centimetres. Samples were immediately placed in air tight plastic bags to transport back to the laboratory. An open ended metal cylinder of 3.8 cm diameter and 23.0 cm length was then manually driven into the exposed sub-surface horizons in the excavated pit. Sub-soil cores were extracted from the cylinder using a hand operated extruder.

6.2.2.2 *Laboratory techniques*

The estimation of microbial biomass was based on a method originally outlined by Amato & Ladd (1988), and modified by Joergensen & Brookes (1990), Ocio & Brookes (1990) and Rowell (1994). The principle assumes that when micro-organisms are killed by chloroform vapour, a proportion of the cell constituents become soluble and thus extractable from the soil as nitrogen ('N'). 'N' is derived from solubilized amino acids and ammonium using potassium chloride solution. The 'N' levels are directly proportional to the biomass initially present in the soil and are estimated by reaction with ninhydrin and measured as a purple complex using a spectrophotometer. Although only approximately one quarter of the biomass-N is released, between-group comparisons are justified as long as conditions are standard for all samples (Rowell 1994).

6.2.2.1.1 Reagents

The ninhydrin reagent, lithium acetate buffer, ethanol-water, nitrogen (leucine) standards and potassium chloride solutions were made up according to the specifications of Rowell (1994).

6.2.2.1.2 Biomass fumigation and extraction

Four 25 g subsamples were obtained from each individual sub-plot core from compacted and undisturbed soils at both soil depths. Two of these subsamples were placed in specimen dishes in a vacuum dessicator containing a beaker filled with 25 ml of chloroform, whilst the other two subsamples were placed in a fume cupboard and left in the open air. The dessicator was evacuated using a vacuum motor pump until the chloroform had boiled for two minutes. This allowed the vapour to penetrate the soil and kill the micro-organisms. The dessicator was sealed and was left overnight in a fume cupboard along with the unfumigated samples. Fumigated and non-fumigated samples were then placed in separate conical flasks with 100 ml of 2 M KCl, and shaken on a mechanical stirrer for 30 minutes. Solutions were then filtered through Whatman No. 42 paper into boiling tubes.

6.2.2.1.3 Estimation of ninhydrin-reactive N

In order to obtain a calibration plot of absorbance against N concentration ($\mu\text{ g ml}^{-1}$), mixtures of 2 ml of each leucine standard and 1 ml of ninhydrin reagent were placed in separate boiling tubes. Tubes were transferred to a boiling water bath for 25 minutes and allowed to cool, after which 20 ml of ethanol-water was added to each standard. After mixing, the absorbance value of each standard was estimated using a spectrophotometer set at a wavelength of 570 nm using 1 cm cells, with distilled water used as a blank. Soil filtrates were made up using the same procedure as the standard, but 2 ml of each extract was added instead of the leucine standard.

The N concentration ($\mu\text{ g ml}^{-1}$) of each extract was then calculated from the calibration line. The difference between non-fumigated and fumigated subsamples was equal to the amount of ninhydrin-reactive N released by fumigation ($\mu\text{ g N ml}^{-1}$). The volume of the extract was 100 ml plus the volume of the water in the soil ($\text{g H}_2\text{O g}^{-1}$ oven-dry soil). This modified extract volume was multiplied by the amount of ninhydrin-reactive 'N' released by fumigation to give the amount of ninhydrin-N ($\mu\text{ g}$). By dividing the amount of ninhydrin-N by the mass of oven-dry soil in the 25 g subsample, the ninhydrin-N ($\mu\text{ g N g}^{-1}$ oven-dry soil) was obtained. Although there is some uncertainty about the factor used to estimate biomass from ninhydrin-reactive N (Rowell 1994), Ocio & Brookes (1990) used the following conversion factors:

- biomass-C = $31 \times \text{ninhydrin-N } (\mu\text{ g g}^{-1} \text{ oven-dry soil})$
- biomass-N = $4.6 \times \text{ninhydrin-N } (\mu\text{ g g}^{-1} \text{ oven-dry soil})$

On average 50 % of the dry biomass is carbon (Rowell 1994, Stalfelt 1973), so:

- biomass (dry matter) = $62 \times \text{ninhydrin-N } (\mu\text{ g g}^{-1} \text{ oven-dry soil})$

Although the procedure does not give absolute values, treatments can be compared with confidence (Rowell 1994).

6.2.3 *Determination of the respiration rate of the microbial biomass*

6.2.3.1 *Sampling in the field*

Heavily compacted and adjacent undisturbed surface and sub-surface soils were randomly sampled at eight time intervals between mid-1995 and mid-1996 in Tocil Wood. Single surface soil cores were extracted from compacted and undisturbed soils using a 10 cm diameter and 10 cm depth root auger. Samples were placed in air tight plastic bags for transportation to the laboratory. An open ended metal cylinder of 3.8 cm diameter and 23 cm length was then manually driven into the exposed subsoil of the excavated pit. Sub-surface soil cores were extracted from cylinders using a hand operated extruder.

6.2.3.2 *Laboratory techniques*

The methodology was adapted from procedures delineated by Rowell (1994), where carbon dioxide respired by micro-organisms is trapped by absorption in NaOH solution. The amount of NaOH solution left after a known time interval is determined via titration with a standard acid. The NaOH solution has a strong affinity for CO₂, so in the actively respiring soil samples the respired CO₂ is readily absorbed. Barium chloride is added to precipitate the sodium carbonate produced in reaction from NaOH absorbing CO₂. The standard acid then reacts with the residual NaOH in the subsequent direct titration.

6.2.3.2.1 Reagents

The sodium hydroxide solution, hydrochloric acid, barium chloride and phenolphthalein indicator were made up following specifications by Rowell (1994).

6.2.3.2.2 Preparation before titration

Two 50 g compacted and undisturbed soil samples from each soil depth were placed in separate 250 ml conical flasks. Individual vials of 2 cm diameter and 8 cm length were filled with 10 ml of 0.3 M NaOH and were immediately placed into each flask which was then tightly bunged. The time of sealing each flask was noted. Two control

flasks with 50 g of sand were also set up, and flasks were incubated in a covered plastic box outside for seven days. In addition, field bulk density measurements in 'g cm⁻³' and soil water content in 'g H₂O per 100 g oven-dry soil' were calculated for each sample using methodology from section 5.2.4.

6.2.3.2.3 Titration with standard acid and calculations

After vials were removed from each respiration flask, the solution was added to a 250 ml conical flask along with 10 ml of distilled water, 10 ml of barium chloride and 6 drops of phenolphthalein indicator. This solution was then titrated with 0.1 M hydrochloric acid until the colour changed from a red-pink to colourless.

Mean titrations of soil and control samples (ml) were obtained, and used to calculate a respiration rate expressed in 'g CO₂ g⁻¹ air-dry soil s⁻¹' (Rowell 1994). Estimations of field soil respiration were made by incorporating the field bulk density measurements at soil depths in compacted and undisturbed zones. The field respiration rate was expressed in 'g CO₂ m⁻² d⁻¹'.

6.2.3.3 *Oxygen content and duration of aerobic conditions*

The duration of aerobic conditions in the absence of gaseous exchange was calculated for all replicates at both soil depths by combining laboratory respiration rates with measurements of bulk density (g cm⁻³) and air-filled porosity (cm³ air cm⁻³ pores) from Chapter 5. The mass of oxygen in the pores was 21 % of the air-filled porosity, and the amount of oxygen in this volume was calculated using the gas equation:

$$pV = nRT$$

Accordingly, the mass of oxygen was expressed in 'g O₂ g⁻¹ soil'.

The maximum duration of respiration if no gas exchange occurred was then calculated by considering respiration rates in terms of laboratory CO₂ production. The duration of aerobic conditions was the amount of oxygen (g O₂ g⁻¹ soil) divided by the rate of use (g O₂ g⁻¹ s⁻¹), expressed in seconds and rounded up to hours.

6.2.4 *Statistical analysis*

Analyses were carried out using SYSTAT 5.2.1.

Chapter 6

PART ONE

**Comparisons of abundance and diversity between compacted
and undisturbed surface soil and litter mesofauna**

6.3 Results

6.3.1 Soil mesofauna abundance and mean population density

From the synopsis of major groups in the two woodland sites, the mean total mesofauna population density in compacted paths of Tocil and Tilehill Woods over the sampling period ranges from 7215 and 9676 organisms per m⁻², to 64891 and 83299 organisms per m⁻² in undisturbed areas.(Table 6.1).

Table 6.1 - Synopsis of mean population density (individuals per m⁻²) from 1995 to 1997 for the most common groups of mesofauna and smaller macrofauna. Population densities of control, trailside and heavily compacted zones are given for Tocil Wood (mull humus) and Tilehill Wood (moder / mor humus).

Group	<i>Tocil Wood</i>			<i>Tilehill Wood</i>		
	Trampled	Trailside	Control	Trampled	Trailside	Control
Total	7215	35013	64891	9676	29156	83299
<i>Saprophagous, zoophagous and microphytophagous mesofauna</i>						
Acari	2780	8636	28774	6111	11103	41793
Collembola	3565	22832	28689	2451	13973	35045
Dermaptera	0	63	85	0	0	0
Psocoptera	0	255	445	0	64	167
<i>Saprophagous macrofauna</i>						
Diplopoda	0	106	467	0	0	159
Isopoda	0	85	297	0	0	21
Gastropoda	0	21	127	0	0	42
Diptera larvae	233	1188	2313	191	1623	1751
Lumbricidae	0	85	212	0	0	0
<i>Zoophagous macrofauna</i>						
Araneae	0	127	403	0	95	229
Pseudoscorpionida	0	148	339	0	101	414
Chilopoda	0	339	361	191	573	668
Opilionida	0	0	21	0	0	0
Coleoptera larvae	106	361	912	95	605	1305

The soils of Tocil Wood are represented by 28 Orders and the soils of Tilehill Wood by 23 Orders. The mull woodland has a higher abundance and diversity of Lumbricidae, Gastropoda, Diplopoda, Isopoda, Pseudoscorpionida, Opilionida,

Chilopoda and adult Coleoptera than the moder / mor woodland (Table 6.1). In contrast, the moder / mor woodland is characterised by lower macrofauna populations and higher mesofauna populations.

In both woodlands, the mean population density in undisturbed areas is greater by an approximate factor of nine than populations in compacted areas. Of the 30 Orders recorded in both sites, 11 are present in the heavily compacted zone, 26 in the edge zone and 28 in the undisturbed control zone. Collembola and Acari are the most abundant fauna groups in all three zones in both woodland sites, but certain groups such as Enchytraeidae are under-represented. The moder / mor soils of Tilehill Wood are dominated by microphytophagous mesofauna groups, whilst the mull soils of Tocil Wood are characterised by a higher proportion of saprophagous macrofauna.

The abundance of the overall mesofauna and the two most common orders of Acari and Collembola throughout the sampling period differ significantly with trampling but not between the two sites (Table 6.2). This suggests that the impact of trampling significantly reduces soil mesofauna population density independently of sites, and thus humus type.

Table 6.2 - Ranked two-way ANOVA and Tukey multiple comparisons for total mesofauna, Acari and Collembola abundance in between 1995 and 1997 in Tilehill Wood and Tocil Wood.

	Total mesofauna			Acari			Collembola		
Source	df	F	p	df	F	p	df	F	p
Site	1	0.7	0.42	1	2.8	0.109	1	0.6	0.44
Path type	2	31.0	>0.001	2	23.9	>0.001	2	12.3	>0.001
Interaction	2	0.2	0.83	2	0.08	0.92	2	0.01	0.99
Significantly Different Treatments^a									
Site	NS			NS			NS		
Path type ^b	(C > T > H)			(C > T > H)			(C, T) > H		

^a - significant at $p \leq 0.05$; NS = not significant

^b - H = heavily compacted trail, T = trail edge, C = control undisturbed soil

The total number of organisms in Orders decreases from depleted populations in trail centres to maximum populations in undisturbed zones (Fig. 6.1). Even comparatively low levels of trampling at path margins have significant negative impacts on total mesofauna population density.

There appears to be no clear sequence of phenological events that is related to seasonality in the undisturbed mor / moder soils of Tilehill Wood. However, fluctuations of total mesofauna populations in the undisturbed mull profile at Tocil Wood are in accordance with key sequences of discernible phenophases over the seasons. A winter minimum of 18589 organisms per m^{-2} is apparent in February 1996, which contrasts markedly with populations during spring (87214 organisms per m^{-2}) and autumn (143490 organisms per m^{-2}).

There are greater numbers of Acari recorded in the moder / mor soils of Tilehill Wood compared to the mull soils of Tocil Wood, but differences are not statistically significant ($p = 0.109$). The patterns of response to trampling shown by Acari is similar to trends in the total mesofauna population, with numbers significantly more abundant in undisturbed zones than compacted zones (Table 6.2). The population density of Acari (m^{-2}) in heavily compacted trail centres and undisturbed soils at the two woodland sites fluctuates widely with the seasons (Fig. 6.2), highlighting the sensitivity of this group to distinct seasonal phenophases especially in mull soils. The population density of heavily trampled zones remains consistently low throughout the entire sampling period, suggesting that the impact of trampling is too severe to allow the population to show clear phenological changes with seasonality.

The population density of Collembola in undisturbed soils is significantly higher than trampled zones (Table 6.2). The seasonal variation in Collembolan population density (organisms per m^{-2}) in heavily compacted and undisturbed zones at the two woodland sites also contrast sharply (Fig. 6.3). The highest numbers are recorded in undisturbed zones at 81103 organisms m^{-2} in May 1996 for Tilehill Wood. Seasonal fluctuations again appear to influence mull Collembolan populations in Tocil Wood, and population densities in heavily trampled zones remain fairly constant and low

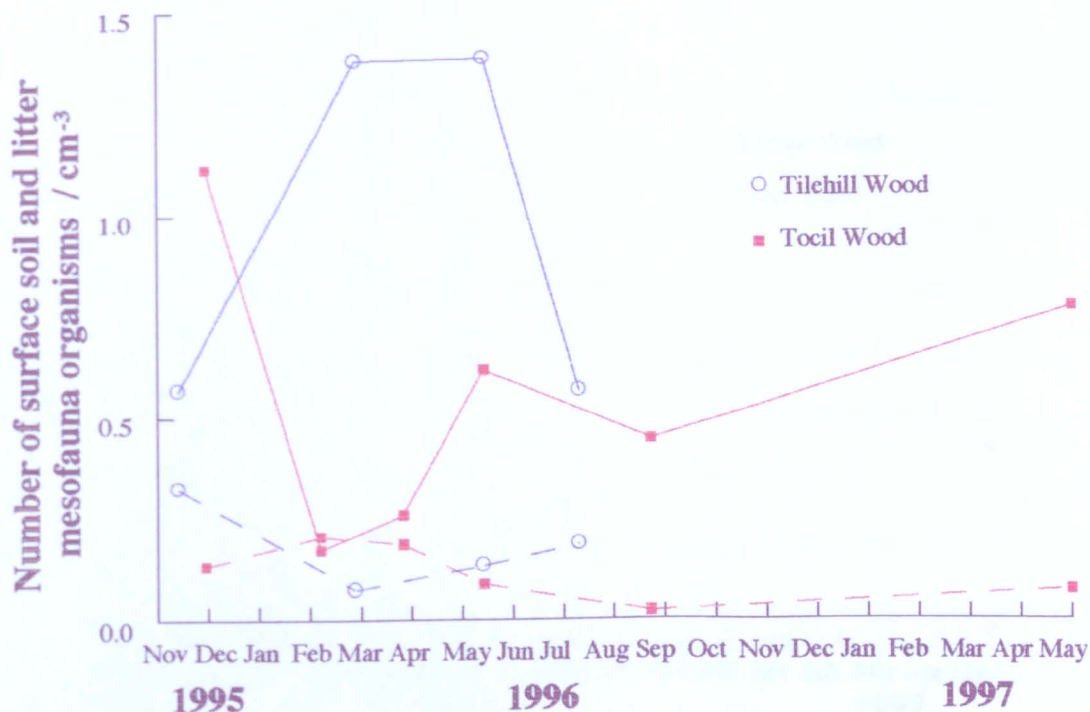


Fig. 6.1 - Seasonal fluctuations in the number of surface litter and soil (0 to 5 cm depth) mesofauna organisms per cm³ in Tocil Wood (deciduous mull) and Tilehill Wood (coniferous moder / mor) in heavily compacted (dashed lines) and undisturbed (plain lines) areas.

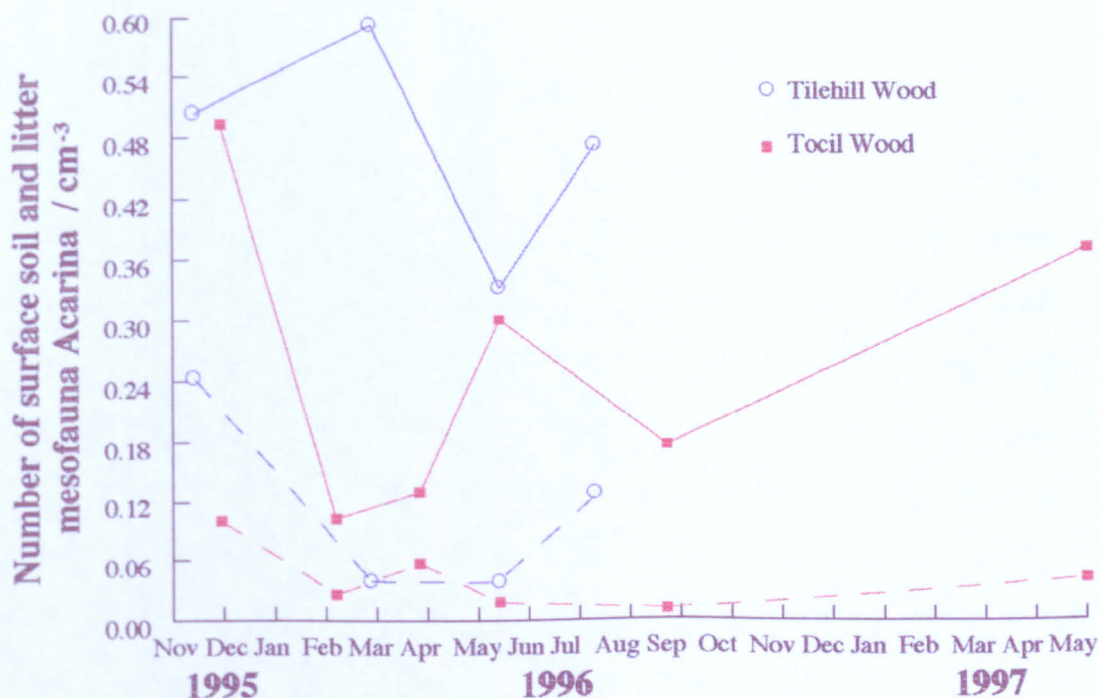


Fig. 6.2 - Seasonal fluctuations in the number of surface litter and soil (0 to 5 cm depth) mesofauna Acarina per cm³ in Tocil Wood (deciduous mull) and Tilehill Wood (coniferous moder / mor) in heavily compacted (dashed lines) and undisturbed (plain lines) areas.

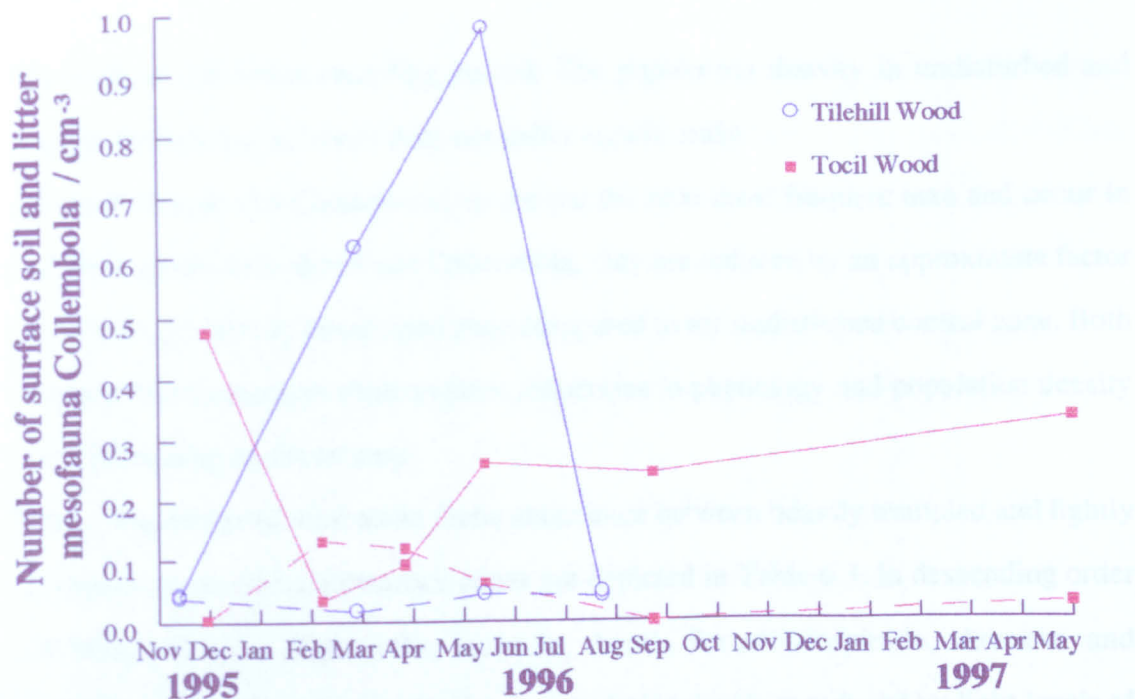


Fig. 6.3 - Seasonal fluctuations in the number of surface litter and soil (0 to 5 cm depth) mesofauna Collembola per cm⁻³ in Tocil Wood (deciduous mull) and Tilehill Wood (coniferous moder / mor) in heavily compacted (dashed lines) and undisturbed (plain lines) areas.

throughout the entire sampling period. The population density in undisturbed and lightly trampled edge zones does not differ significantly.

Dipteran larvae and Coleopteran larvae are the next most frequent taxa and occur in all three zones. Like Acari and Collembola, they are reduced by an approximate factor of nine in the heavily compacted zone compared to the undisturbed control zone. Both Diptera and Coleoptera show evident reductions in phenology and population density with increasing levels of wear.

The comparisons of total mean fauna abundance between heavily trampled and lightly trampled zones with undisturbed zones are depicted in Table 6.3. In descending order of susceptibility, Diplopoda, Isopoda, Acari, Pseudoscorpionida, Araneae and Coleoptera all have at least half of their population densities reduced by light levels of trampling at path margins. The majority of the Insecta Orders are also absent in heavily trampled zones and so are extremely intolerant of trampling. However, Collembola, Coleoptera and especially Chilopoda are more tolerant of low levels of trampling.

6.3.2 *Use of Acari body length as a bioindicator of soil trampling*

Although Acari are not identified beyond the Order level, the majority of small mites found in the heavily compacted zone belong to the Oribatida family. In the heavily trampled zone, small sized Acari (< 0.2 mm) are significantly more abundant than moderate (0.2 - 0.5 mm) and large (> 0.5 mm) Acari (Table 6.4). In path margin and undisturbed zones there are no significant differences between any of the three size categories. Thus, obvious Acari size distribution changes occur in soils susceptible to heavy compaction only, with moderate and large size categories being steadily eradicated as trampling increases.

Table 6.3 - Mean relative reduction (expressed as the percent decrease of undisturbed populations) in total soil fauna numbers of heavily trampled zones (path centre) and lightly trampled zones (path edge) compared with undisturbed zones as categorised by Order (pooled for both sites and over the entire sampling period).

Order	Path edge vs. Undisturbed	Path centre vs. Undisturbed
Chilopoda	11 %	81 %
Diptera	31 %	90 %
Collembola	42 %	91 %
Coleoptera	56 %	91 %
Araneae	65 %	-
Pseudoscorpionida	67 %	-
Acari	72 %	87 %
Isopoda	73 %	-
Diplopoda	83 %	-
Overall	57 %	89 %

Table 6.4 - Kruskal-Wallis one way ANOVA and non-parametric Tukey-like multiple comparisons (using Nemenyi's test) to test for differences in Acari body length abundance between surface compacted, edge and undisturbed litter and soil populations. Samples were taken between 1995 and 1997 and pooled for both Tocil and Tilehill Woods.

<i>Compacted zone</i>		<i>Edge zone</i>		<i>Control zone</i>	
H	p	H	p	H	p
12.2	>0.002	0.6	0.755	1.2	0.555
Significantly Different Treatments^a					
Small > (Moderate, Large)		NS		NS	

^a - significant at $p \leq 0.05$, NS = not significant; **Small** = small mite size (< 0.2 mm), **Moderate** = moderate mite size (0.2 to 0.5 mm), **Large** = large mite size (> 0.5 mm)

The relative proportions of mite size categories change according to season, but general trends remain similar across all four (Table 6.5). When visitor densities are at a maximum in summer, the reduced community of Acari is dominated almost entirely

by small size mites. For example, the highest proportion of small Acari occurs during summer at 79 % in heavily compacted areas, and the lowest in winter at 60 %. In winter the size distribution in heavily compacted zones is less marked, and rises to a seasonal maximum 18 % in the proportion of large size Acari. Size distribution patterns in autumn and spring remain similar. The trend of a higher proportion of small Acari in summer is also borne out in lightly trampled trailside samples. Even here, it is obvious that trampling operates as a major limiting factor because the relative proportion of small Acari attains a seasonal maximum of 44 % in summer. Acari size does not differ significantly between control and edge zones in any season, so the proportions of each of the three size categories in edge and control zones are approximately equal, but with a higher relative proportion of large Acari in uncompacted soils. Thus, variation in mite size is strongly influenced by seasonal visitor patterns.

Table 6.5 - Relative percent proportions of small (< 0.2 mm), moderate (0.2 - 0.5 mm) and large (> 0.5 mm) Acari based on their body length size. Overall percent proportional means in spring, summer, autumn and winter samples in heavily compacted, trailside and undisturbed surface soil and litter zones pooled for Tilehill Wood and Tocil Wood.

	<i>Heavily compacted zone</i>			<i>Trailside zone</i>			<i>Undisturbed zone</i>		
Season ^a	Small	Moderate	Large	Small	Moderate	Large	Small	Moderate	Large
Overall	67.2	22.2	10.6	34.4	36.8	28.8	29.5	34.3	36.2
Spring	66.2	20.3	13.5	32.0	38.2	29.8	28.0	39.2	32.8
Summer	78.6	16.1	5.3	43.6	32.5	23.9	26.3	43.9	29.8
Autumn	65.0	25.1	9.9	36.0	41.0	23.0	30.0	32.5	37.5
Winter	60.0	23.3	17.7	32.9	32.9	34.2	23.8	30.9	45.3

^a - Overall = mean for entire sampling period; spring = March, April, May; summer = June, July, August; autumn = September, October, November; winter = December, January, February

This data was used to synthesise a bioindicator index which is given in section 7.3.3.

6.3.3 Relationship of soil mesofauna population density with soil variables and visitor numbers

The ranked correlations of all major soil mesofauna groups with estimates of visitor numbers, pH and bulk density are negative and highly significant (Table 6.6). Most other correlations are positive and significant. Coleoptera and Diptera larval population densities show the highest correlations with air-filled porosity. Indeed, the latter group show the highest significant associations with all of the other soil variables.

Table 6.6 - Spearman rank correlation coefficients (r_s) computed for paired relationships between total mesofauna, Acari, Collembola, Diptera larvae and Coleoptera larvae population density (organisms m⁻²) with bulk density (g cm⁻³) (**BD**), total porosity (%) (**POR**), organic matter (%) (**OM**), pH (**pH**), gravimetric water content (g H₂O g⁻¹ soil) (**GWC**), water-filled porosity (cm³ H₂O cm⁻³ soil) (**WFP**), air-filled porosity (cm³ air cm⁻³ soil) (**AFP**) and cumulative visitor numbers (wear class per year) (**VIS**).

	BD	POR	OM	pH	GWC	WFP	AFP	VIS
All mesofauna	-0.80	0.81	0.66	-0.62	0.59	0.28	0.62	-0.78
Acari	-0.70	0.72	0.64	-0.54	0.57	0.34	0.44	-0.70
Collembola	-0.68	0.68	0.50	-0.45	0.50	0.24	0.56	-0.62
Diptera	-0.75	0.76	0.69	-0.72	0.63	0.36	0.58	-0.56
Coleoptera	-0.69	0.67	0.53	-0.50	0.58	0.36	0.45	-0.52

All $p \leq 0.05$ except **WFP** (all non-significant)

A comparison of Acari abundance and organic matter in the heavily trampled zone only also yields a significant positive correlation ($r_s = 0.65$; $n = 10$). Thus, there appear to be gradients of change related to soil organic matter even within zones of high degradation.

Linear and curvi-linear regression models approximate the relationship between data transformed mean population density of the most abundant mesofauna groups and the

independent indicators of trampling intensity (bulk density as a measure of soil compaction and visitor numbers) (Table 6.7). The proportion of the total variation in population density that is explained by the regression models is greatest for the pooled mesofauna population density. This suggests that the best indicator of trampling disturbance is the whole mesofaunal community. In terms of individual groups, the coefficients of variation remain high with both indicators of trampling intensity for Acari, validating their use as bioindicators of soil compaction. Coleoptera larvae have the poorest fit to the regression models, but these models are still statistically significant.

Table 6.7 - Linear and polynomial (second-order) regression models that approximate the relationship between total mesofauna (\log_{10} transformed), Acari (\log_{10} transformed), Collembola (\log_{10} transformed), Diptera larvae ($\sqrt{}$ transformed) and Coleoptera larvae (\log_{10} transformed) population density (organisms per m^{-2}) with bulk density (g cm^{-3}) and cumulative visitor numbers (per annum) for Tocil Wood.

<i>Group</i>	<i>Bulk density</i>	<i>r²</i>	<i>Visitor numbers</i>	<i>r²</i>
<i>Mesofauna</i>				
Linear	$y = 6.38 - 1.81x$	0.65	$y = 4.65 - 0.0004x$	0.53
Polynomial	$y = 4.95 + 0.75x - 1.10x^2$	0.67	$y = 4.80 - 0.0013x + (4.1 \times 10^{-7})x^2$	0.67
<i>Acari</i>				
Linear	$y = 5.84 - 1.69x$	0.52	$y = 4.21 - 0.0004x$	0.38
Polynomial	$y = 5.20 - 0.54x - 0.50x^2$	0.52	$y = 4.41 - 0.0016x + (5.4 \times 10^{-7})x^2$	0.60
<i>Collembola</i>				
Linear	$y = 6.08 - 1.93x$	0.48	$y = 4.26 - 0.0005x$	0.47
Polynomial	$y = 5.20 - 0.36x - 0.68x^2$	0.48	$y = 4.37 - 0.037x + (2.9 \times 10^{-7})x^2$	0.52
<i>Diptera</i>				
Linear	$y = 102.4 - 64.1x$	0.58	$y = 40.8 - 0.015x$	0.44
Polynomial	$y = 102.6 - 64.37x + 0.12x^2$	0.58	$y = 44.5 - 0.037x - 0.00001x^2$	0.50
<i>Coleoptera</i>				
Linear	$y = 4.07 - 1.26x$	0.38	$y = 2.87 - 0.00028x$	0.27
Polynomial	$y = 4.79 - 2.60x + 0.60x^2$	0.38	$y = 2.95 - 0.0008x + (2.3 \times 10^{-7})x^2$	0.33

The polynomial model fits a curvilinear function to the data, so the greatest changes in population loss occurs most rapidly at low levels of each of the indicators of trampling intensity. Utilising the mesofauna model, a 50 % drop from an upper limit of 1500 passes in mean mesofaunal population density is caused by approximately 200 visitor passes.

Chapter 6

PART TWO

**Comparisons of microbial biomass and respiration rates
in compacted and undisturbed woodland soils**

6.4 Results

6.4.1 Microbial respiration rates

6.4.1.1 Laboratory and field respiration rates

Mean laboratory soil respiration rates ($\text{g CO}_2 \text{ g}^{-1}$ air-dry soil) are significantly higher in surface soils than sub-surface soils in both compacted and undisturbed samples over the duration of the sampling period (Fig. 6.4). In general, respiration rates are also highest in compacted soils when compared to undisturbed soils, but differences between samples at both soil depths are not significant (Table 6.8). Upon conversion to field respiration rates ($\text{g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$) (Fig. 6.5), only the compacted surface soils differ significantly from the other samples (Table 6.8).

Table 6.8 - Kruskal-Wallis one way ANOVA and non-parametric Tukey-like multiple comparisons (using Nemenyi's test) for laboratory and field respiration rates in compacted and undisturbed soils surface and sub-surface between 1995 and 1996 in Tocil Wood.

<i>Laboratory Respiration Rates</i>				<i>Field Respiration Rates</i>			
n	k	H	p	n	k	H	p
8	4	24.3	> 0.001	8	4	21.5	> 0.001
Significantly Different Treatments^a							
(H, C) > (h, c)				H > (C, h, c)			

^a - significant at $p \leq 0.05$; H = heavily trampled surface soil, C = undisturbed surface soil, h = heavily trampled sub-surface soil, c = undisturbed sub-surface soil.

Seasonal variation in laboratory and field respiration rates in trampled and undisturbed soils reaches a peak in March and May of 1996. A maximum respiration rate of $4.9 \times 10^{-9} \text{ g CO}_2 \text{ g}^{-1}$ air-dry soil and $56.3 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ is recorded in surface compacted soils in May 1996. This contrasts with a minimum of $4.0 \times 10^{-11} \text{ g CO}_2 \text{ g}^{-1}$ air-dry soil and $0.6 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ in undisturbed sub-surface soils in

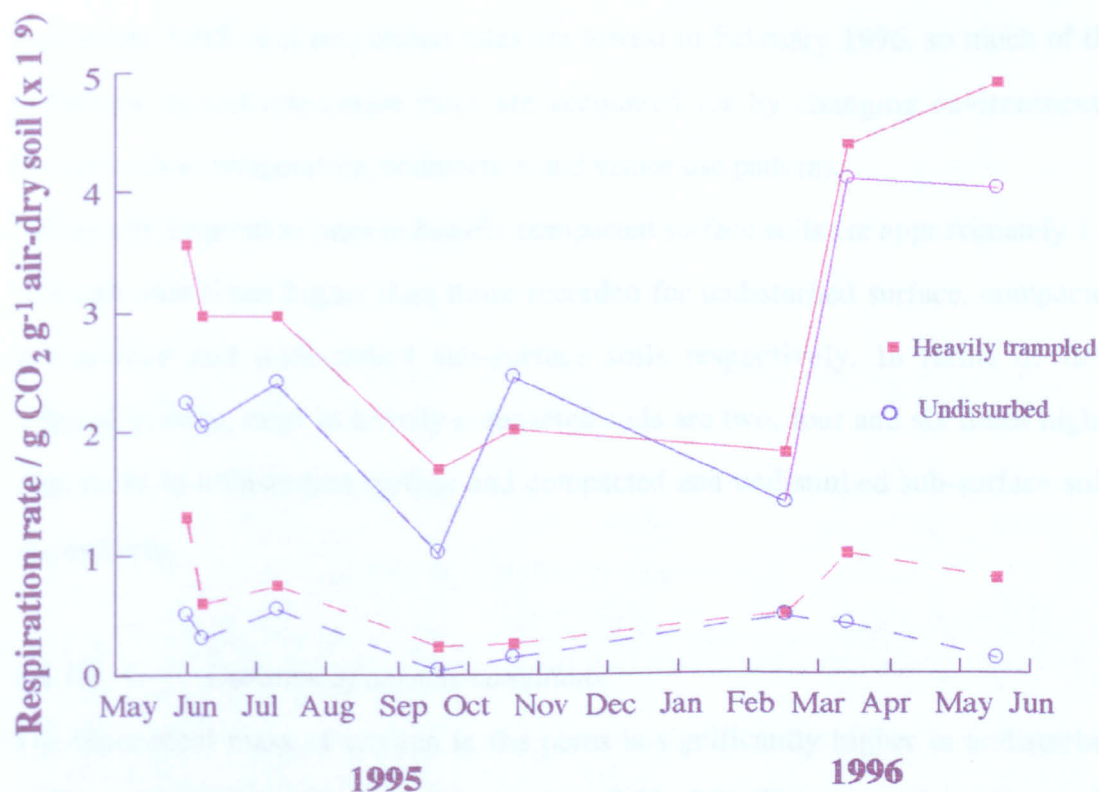


Fig. 6.4 - Seasonal variation in microbial respiration rates in heavily trampled and undisturbed surface 0 - 10 cm depth (solid lines) and sub-surface 10 - 30 cm depth (dashed lines) soils during 1995 and 1996 in Tocil Wood.

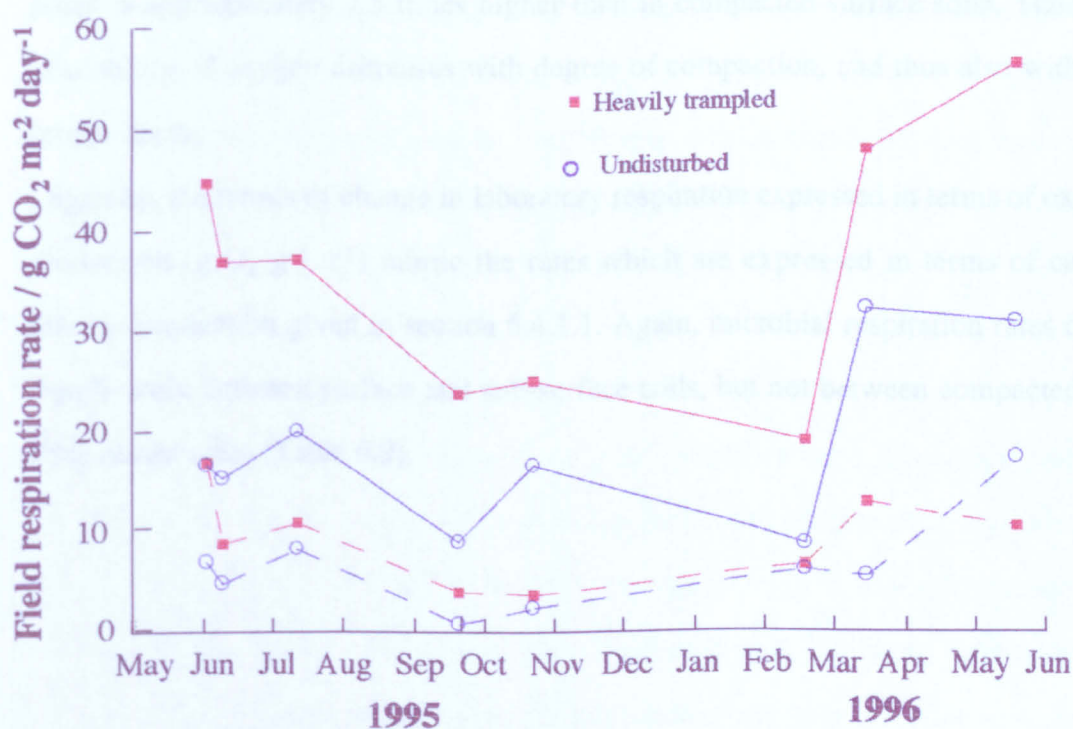


Fig. 6.5 - Seasonal variation in field microbial respiration rates in heavily trampled and undisturbed surface 0 - 10 cm depth (solid lines) and sub-surface 10 - 30 cm depth (dashed lines) soils during 1995 and 1996 in Tocil Wood.

September 1995. Soil respiration rates are lowest in February 1996, so much of the variations in soil respiration rates are accounted for by changing environmental factors such as temperature, compaction and visitor use patterns.

Laboratory respiration rates in heavily compacted surface soils are approximately 1.2, five and nine times higher than those recorded for undisturbed surface, compacted sub-surface and undisturbed sub-surface soils respectively. In terms of field respiration rates, rates in heavily compacted soils are two, four and six times higher than those in undisturbed surface and compacted and undisturbed sub-surface soils respectively.

6.4.1.2 *Duration of aerobic conditions*

The theoretical mass of oxygen in the pores is significantly higher in undisturbed surface soils than in all other soil samples (Table 6.9). The mass of oxygen in the pores does not differ significantly between compacted surface soils and compacted and undisturbed sub-surface soils. The oxygen content in undisturbed surface soil pores is approximately 7.5 times higher than in compacted surface soils. Thus, the availability of oxygen decreases with degree of compaction, and thus also with soil profile depth.

Logically, the trends of change in laboratory respiration expressed in terms of oxygen production ($\text{g O}_2 \text{ g}^{-1} \text{ s}^{-1}$) mimic the rates which are expressed in terms of carbon dioxide production given in section 6.4.1.1. Again, microbial respiration rates differ significantly between surface and sub-surface soils, but not between compacted and undisturbed areas (Table 6.9).

Table 6.9 - Kruskal-Wallis one way ANOVA and non-parametric Tukey-like multiple comparisons (using Nemenyi's test) for mass of oxygen in the pores respiration rate (in terms of oxygen production), and the duration of aerobic conditions in surface and sub-surface compacted and undisturbed soils between 1995 and 1996 in Tocil Wood.

Mass of oxygen (g O ₂ g ⁻¹ soil)		Respiration rate (g O ₂ g ⁻¹ s ⁻¹)		Aerobic duration (hours ⁻¹)	
H	p	H	p	H	p
20.0	>0.001	23.1	>0.001	17.2	>0.001
Significantly Different Treatments^a					
C > (H, h, c)		(H, C) > (h, c)		(C, c, h) > H	

^a - significant at $p \leq 0.05$; **H** = heavily trampled surface soil, **C** = undisturbed surface soil, **h** = heavily trampled sub-surface soil, **c** = undisturbed sub-surface soil.

In theoretical conditions of inhibited gaseous exchange, the duration of aerobic conditions is significantly shorter in compacted surface soils when compared to undisturbed surface soils (Table 6.9). Indeed, the duration of aerobic conditions is low and constant in compacted soils across the sampling period, reaching a maximum of 4.7 hours in October 1995 and a minimum of 0.2 hours in March 1996 (Fig. 6.6). Conversely, the duration of aerobic conditions in undisturbed surface soils is on average a factor of eleven times higher, reaching a maximum in September 1995 at 35.1 hours and a minimum in March 1996 of 4.8 hours.

6.4.2 Microbial biomass rates

Microbial biomass (dry matter) rates (μ g g⁻¹ oven-dry soil) of surface soils are significantly higher than rates in sub-surface soils in both compacted and undisturbed soils (Table 6.10). In contrast to the soil respiration rates, microbial biomass (dry matter) is higher in undisturbed soils than compacted soils. However, differences are not significant between both compacted and undisturbed soils at the two soil depths (Fig. 6.7). Thus, there is a reduction in biomass (and thus numbers) of soil micro-organisms in trampled woodland soils.

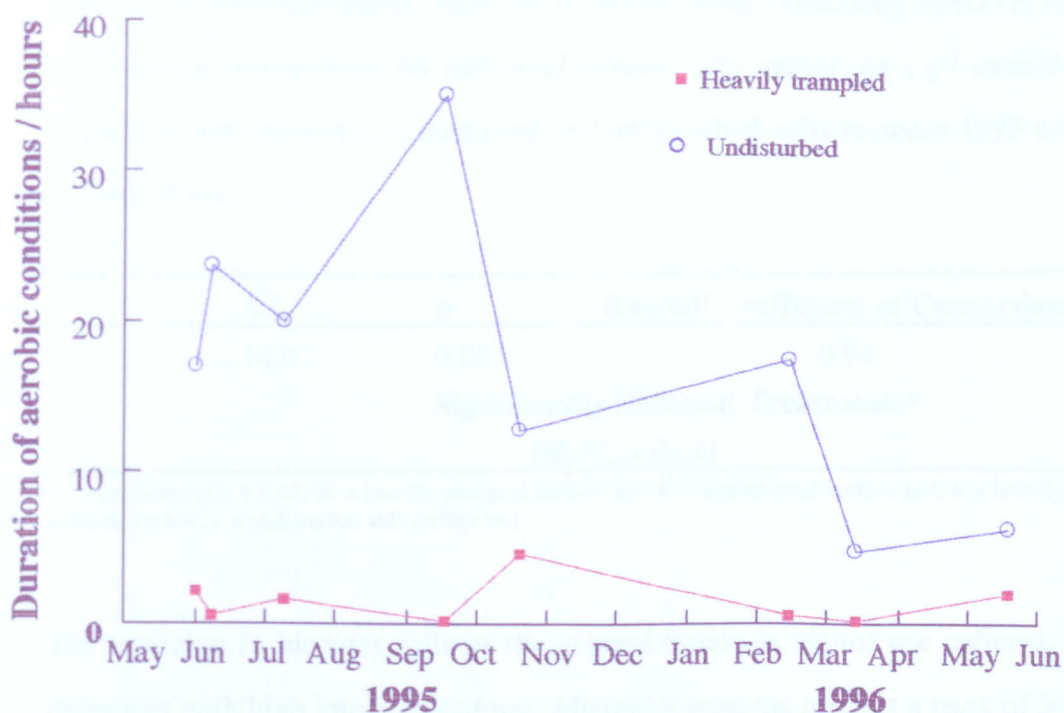


Fig. 6.6 - Seasonal variation in the duration of aerobic conditions in heavily trampled and undisturbed surface 0 - 10 cm depth (solid lines) soils during 1995 and 1996 in Tocil Wood.

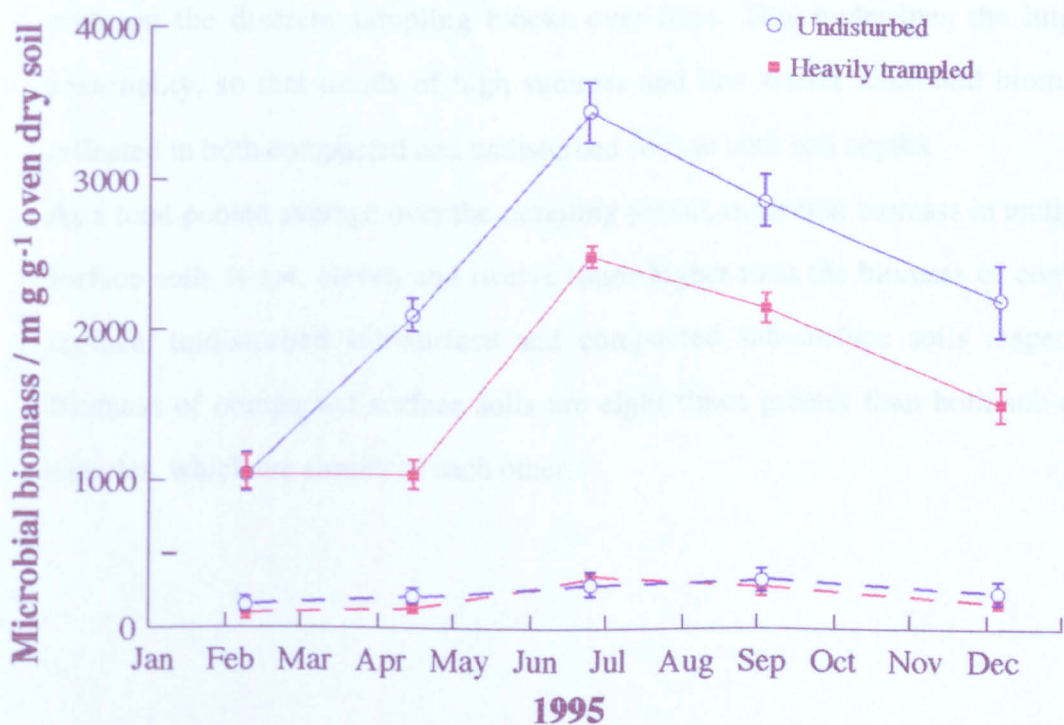


Fig. 6.7 - Seasonal changes in mean microbial biomass (dry matter) in heavily trampled and undisturbed surface (solid lines) (0 to 10 cm depth) and sub-surface soils (dashed lines) (10 - 30 cm depth) during 1995 for Tocil Wood. Vertical bars represent one standard error above and below the mean.

Table 6.10 - Non-parametric repeated measures using Friedman's ANOVA by ranks and multiple comparisons for microbial biomass (dry matter) ($\mu\text{ g g}^{-1}$ oven-dry soil) in surface and sub-surface compacted and undisturbed soils between 1995 and 1996 in Tocil Wood.

X^2_r	p	Kendall Coefficient of Concordance (W)
14.0	0.003	0.94
Significantly Different Treatments^a		
(H, C) > (h, c)		

^a - significant at $p \leq 0.05$; H = heavily trampled surface soil, C = undisturbed surface soil, h = heavily trampled sub-surface soil, c = undisturbed sub-surface soil.

The variation in biomass follows the general trends in visitor use patterns, and so decreases with high intensities of use. Microbial biomass reaches a peak of $3437\ \mu\text{ g g}^{-1}$ oven-dry soil in undisturbed surface soils in June 1995, and falls to a minimum of $76\ \mu\text{ g g}^{-1}$ oven-dry soil in compacted sub-surface soils in February 1995. The high Kendall coefficient of concordance shows that there is a significant association amongst the discrete sampling blocks over time. This underlines the impact of seasonality, so that trends of high summer and low winter microbial biomass are reflected in both compacted and undisturbed soils at both soil depths.

As a total pooled average over the sampling period, microbial biomass in undisturbed surface soils is 1.4, eleven and twelve times higher than the biomass of compacted surface, undisturbed sub-surface and compacted sub-surface soils respectively. Biomass of compacted surface soils are eight times greater than both sub-surface samples, which are similar to each other.

Chapter 7

GENERAL DISCUSSION

Chapter 7

PART ONE

The impact of recreational trampling on woodland vegetation

7.1 Discussion

This first part of the discussion examines the impact of recreational trampling on vegetation by drawing from the results of the field survey (Chapter 2), the experimental trampling trials (Chapter 3) and the simulated trampling experiments (Chapter 4).

7.1.1 *Impact of recreational trampling on the physiognomic characteristics of woodland vegetation*

7.1.1.1 *Impoverished species diversity and number*

There is a sharp decline in both species diversity and number with moderate to high levels of trampling. Diagrammatic representations of vegetation zonation across typical woodland trails are sketched for spring (Fig. 7.1) and summer (Fig. 7.2) surveys. In both summer and spring, diversity is consistently higher at trail margins than in undisturbed or trail centre zones. The response in the total number of species in each wear class follows a similar pattern to diversity, with peak numbers at trail margins. This evidence concurs with observations on plant community structure along forested cliff edges by Parikesit *et al.* (1995), and with work by Hall & Kuss (1986) and Dale & Weaver (1974).

Low levels of trampling keep trail margin vegetation in a dynamic, immature stage, and ensures the continual survival of species such as *Deschampsia flexuosa*, *Holcus spp.*, *Dactylis glomerata*, *Ranunculus ficaria* and *Viola riviniana*. These species appear to thrive in the unique microclimatic conditions imparted by the elimination of tall, shady competitors by trampling. The profusion of woodland wildflowers such as *Oxalis acetosella*, *Ranunculus ficaria* and *Stellaria holostea* at trail margins backs Westhoff's (1967) claim that many species of botanical significance occur on paths in areas of light or medium trampling pressure. Indeed, Scott-Williams (1967) reflected that rare plants are commonly seen on the periphery of woodland trails.

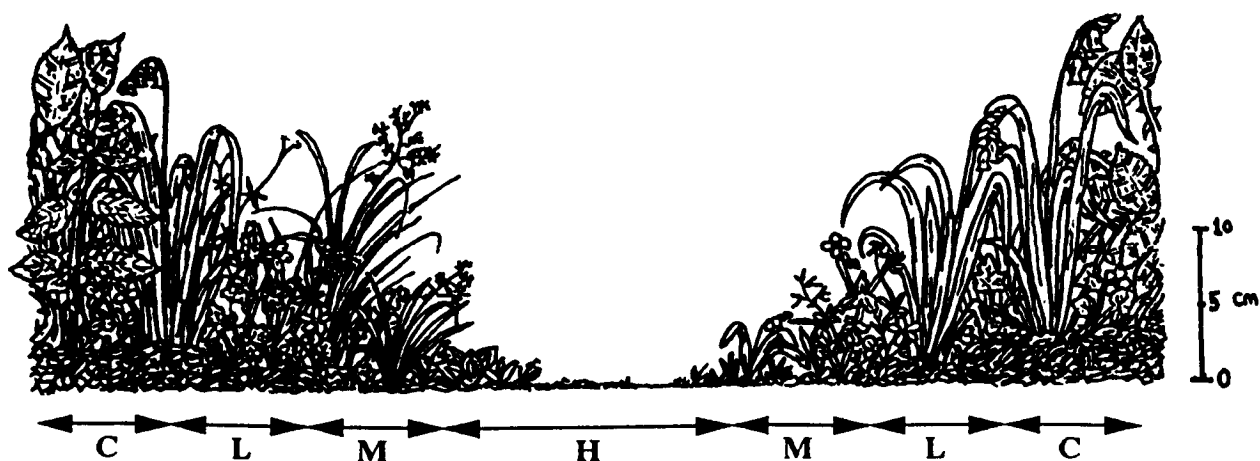


Fig. 7.1 - Zonation across a typical woodland trail showing commonly occurring species during spring, (H = heavily trampled zone; M = moderately trampled zone; L = lightly trampled zone; C = control undisturbed zone).



Fig. 7.2 - Zonation across a typical woodland trail showing commonly occurring species during summer, (H = heavily trampled zone; M = moderately trampled zone; L = lightly trampled zone; C = control undisturbed zone).

The increase in light availability during summer, and limited recreational use in spring, are likely to be main factors responsible for the higher diversity in trailside plots compared to undisturbed areas. Much of the differentiation between trailside and off-trail plots is also as a consequence of subordinate flora being outcompeted for resources by trees, shrubs and homogeneous field layer stands of *Rubus fruticosus* agg., *Pteridium aquilinum* and *Dryopteris* spp. in undisturbed areas. Although the selective forces of trampling are weaker on trail edges compared to trail centres, fluctuating levels of trampling and intense inter-specific competition help to restrict native trailside species to small populations that are patchily distributed. As light levels of trampling appear to create enhanced conditions for species to exploit path margins, the creation of new paths through undisturbed vegetation will increase diversity in areas which would normally only be dominated by a limited number of species.

7.1.1.2 Vegetation cover

7.1.1.2.1 Eradication of cover

Recreational trampling is directly responsible for the acute reduction in cover of vegetation along trails, with the high seasonal visitor use during summer and autumn directly responsible for the pronounced affect on vegetation cover. Trampling reduces vegetation cover of individual species, with continual trampling completely eradicating them or even the whole sub-community. The reduction in plant cover on woodland paths and tracks recorded in this study has been noted by others (e.g.: Cole 1985, 1987, 1988, 1993, Cole & Trull 1992, Ingellog *et al.* 1977), as has the curvilinear response of cover loss with trampling intensity (e.g.: Cole 1987, 1995a, Kellomaki 1973, Kellomaki & Saastamowen 1975, Kuss & Hall 1991).

In all seasons, ground vegetation maintains a maximum coverage in conditions of partial shade along trail edges. During spring, the enhanced coverage of vernal and common species in all wear classes is as a consequence of the increase in sunlight and

moisture, and the lack of a developed overstorey canopy. So much so, that on some routes even heavily trampled zones possess a thick coverage of a wide range of species.

The use of plant cover to convey the vulnerability of sub-community vegetation types to trampling is discussed in section 7.1.2.

7.1.1.2.2 Ordination

Multi-variate ordination using vegetation cover values suggests that 'visitor numbers' is the sole variable that significantly contributes to the explanation of the first axis. This provides ~~conclusive~~ evidence that axis one represents an 'index of response to trampling'. For example, as axis one increases, the proportion of trampling tolerant species such as *Poa spp.* and *Plantago major* also increase. The relationships of the axis with the environmental variables indicates that in summer, species tolerant of trampling occur along open, poorly vegetated trails that are characterised by eroded, dry soils which are low in organic matter.

However, insufficient information exists with which to isolate any single factor that is responsible for the pattern shown in the second axis. Axis two appears to exert influences concentrated on vegetation in undisturbed areas, so is of secondary importance in this investigation. Factors not accounted for in this survey are probably reflected in this axis, e.g.: plant competition, succession, habitat preferences including canopy stratification and other soil properties.

7.1.1.3 *Reduction in vegetation height*

Tall species are conspicuously absent from moderately and heavily trampled areas, and a rapid decrease in vegetation height occurs at low levels of trampling. The physical action of treading injures plants by either bending stems, leaves and tillers near to the soil surface, or breaking them off completely. The decrease in the height of plants that are continually trampled also illustrates that where plants do survive, growth rates are much subdued. Many plants of low stature are favoured in worn

areas because the leaves are positioned at ground level, affording protection to perennating tissues.

By combining the findings of this study with observations by Sun & Liddle (1993a) and Makhdoum & Khorasani (1988), tall stature is clearly a major disadvantage in the ability to tolerate trampling. Leney (1974) even suggested that tall statured plants will only survive in untrampled areas. This study concludes that vegetation height has great potential to be used as a criterion to assess the degree of recovery, validating its use in Chapter 3 and 4 as an indicator of trampling.

The extent of height reduction is more pronounced at low levels of use than most of the other morphological parameters measured, especially in the upright *Pteridium aquilinum* stand. Indeed, low levels of simulated trampling reduces plant stature by approximately half compared to untrampled plants. In the field survey, comparisons of vegetation height for individual species between wear classes yield the greatest proportion of statistically significant differences. This cumulative evidence suggests that the response of plant height is a particularly sensitive plant morphological characteristic, so damage to vegetation is most clearly shown by the persistent reduction in height in impacted areas (Liddle 1975b).

The variation in response of plant height to trampling is high across the range of species tested, and some species are more susceptible than others. Sun & Liddle (1993a) also found a gradient of change in plant height related to trampling level in thirteen Australian subtropical species. Some species can increase in height during periods between frequent trampling, favouring their continual survival along trails, e.g.: *Plantago major*, *Poa pratensis* and *Plantago lanceolata*.

Plant height in grasses appears to be dependent upon the response of tiller expansion to physical damage. The reduction in plant height of trampled plants of *Poa pratensis* and *Lolium perenne* is as a consequence of their flexible tillers being bent towards the soil surface. The loss in plant height of *Brachypodium sylvaticum*, *Deschampsia flexuosa* and *Holcus lanatus* is more of a consequence of direct defoliation as stems and tillers are broken off or injured. Thus, there appears to be a positive relationship

between the ability of a plant species to resist damage and stem flexibility and toughness.

Mercurialis perennis and most fern species undergo the highest reduction in height as a consequence of low and heavy trampling. This implies that tall species undergo a greater proportional decrease in plant height than do short species. Indeed, this study agrees with Cole (1988) and Kuss (1986), by suggesting that tall stature implies poorer resistance to trampling. However, there are notable exceptions; some shorter species in their vegetative state, such as *Silene dioica*, are equally intolerant of light or heavy trampling.

7.1.1.4 *Changes to leaf and tiller architecture*

7.1.1.4.1 Fewer, thinner, shorter and smaller leaves

Both slightly and heavily trampled plants have fewer leaves than undisturbed plants, with losses attributed to direct abrasive damage to leaves, to the eradication of leaf bearing structures such as stems, stolons and tillers and to the inhibition of growth rates that readily suppress the ability of plants to generate new leaves. The negative relationship between the number of leaves and trampling intensity suggested by this study was also found by Bratton (1985).

The wearing of leaves occurs most rapidly with woodland species compared to those species typical of trail centres. For instance, *Plantago major*, *Poa pratensis*, *Lolium perenne* and *Deschampsia cespitosa* have the highest relative number of leaves after heavy trampling, and *Teucrium scorodonia*, *Mercurialis perennis*, *Deschampsia flexuosa* and *Silene dioica* the lowest. As the former group have the highest resistance indices, and the latter group the lowest, there is a positive relationship between plant resistance and the ability to maintain injured leaves. The ability of leaves and leaf bearing structures to tolerate physical trampling impacts are related to the overall vulnerability of leaf anatomy and the brittleness of stems.

The majority of species surviving in trampled areas of woodland trails possess tough, narrow leaves and are typically grasses. Proportional reductions in leaf widths occur with increasing trampling intensity, with a greater relative loss in broad leaved species compared to narrow leaved species. For example, the relative leaf width after heavy trampling is greater for grass species at 69 % than other species at 55 %. Light levels of trampling may even stimulate an increase in leaf width of trampled tolerant species compared to undisturbed plants, e.g.: *Lolium perenne*.

Few species with broad leaves occur in heavily and moderately trampled areas, and those that do are very much reduced. For instance, the leaf width of *Plantago major* is significantly reduced in summer, declining by an approximate factor of five from lightly to heavily trampled areas. Leaf widths of other moderately and highly resistant species appear to reach equilibrium with the trampling pressure, and so remain constant under continual trampling.

Vulnerable species such as *Mercurialis perennis* and *Silene dioica* undergo a slight decrease in leaf width throughout the treatment period, implying that trampling inhibits the normal expansion of leaf width. Both species have delicate, wide leaves, confirming Grabherr's (1982) supposition that broad leaves are a major disadvantage in the resistance of plants to trampling.

All species show a decrease in leaf length in response to trampling in this study, but declines in leaf length are particularly marked in long leaved monocotyledonous species. For example, the leaf lengths of *Deschampsia cespitosa* recorded in the summer field survey and *Hyacinthoides non-scripta* in the spring field survey are both an approximate factor of six times shorter in the heavily trampled trail centre than in undisturbed areas. The general response confirms trends reported in a previous study by Bratton (1985), who noted a similar reduction in the mean length of the longest leaves of two trampled orchid species.

Leaf lengths are shorter in heavily trampled plants than lightly trampled plants for the majority of species, and the relative leaf lengths of *Mercurialis perennis* and *Silene dioica* are severely reduced after only light levels of trampling. The rapid reductions

in leaf length under low levels of trampling are attributed to the fragility of leaf morphology. A slow growth rate occurs in species with tough leaves such as *Plantago major* and *Deschampsia cespitosa*, which mainly utilise a resistance strategy to tolerate trampling. Indeed, for both of these species, relative leaf length is very similar after heavy and light trampling, and the leaf lengths of both heavily trampled species increases slightly throughout the treatment period.

Leaf size is readily suppressed by even low levels of trampling. Large leaved species such as *Hyacinthoides non-scripta* appear to be more readily damaged than small leaved species. Plants quickly become stunted, and any surviving leaves are riddled with necrotic patches and scars. Parameters such as leaf strength control the rate of reduction in leaf area. Leaf size is one of the morphological parameters that has the greatest influence on plant resistance to trampling (Kuss 1986).

A microphyllous aspect in some species in response to trampling is as a consequence of the formation of fewer and smaller cells, with cell division processes extensively inhibited (Grabherr 1983). In this study, after several weeks of trampling, the leaf morphology of *Plantago major* and *P. lanceolata* begins to attain a crumpled irregular shape. This is probably as a consequence of deformation of the leaf palisade cells (Goryshina 1984). As the cells of *P. major* are also strengthened with tuberin or hemicellulose rather than the more rigid lignin (Grabherr 1983, Liddle 1991), the stability of internal leaf structure is another factor controlling response. So for resistant species, small cells (< 0.1 mm) may be an advantage to survive compressive forces, in contrast to vulnerable species with large cells (Liddle 1991, Shields & Dean 1949 in Yorks *et al.* 1997). Indeed, those species that are easily damaged by trampling such as *Mercurialis perennis* possess leaves with thin walled epidermis and large cells and air spaces (Mukerji 1936).

7.1.1.4.2 Changes in the number of tillers

Trampling induces a variable response amongst different grass species in terms of the production of tillers. *Deschampsia cespitosa* and especially *Lolium perenne* exhibit a

marked increase in tillering capacity under low levels of trampling, whilst tiller number remains similar between control and lightly trampled plants of *Poa pratensis* and *Holcus lanatus*. Sun & Liddle (1993c) also found that slightly trampled plants of *Lolium perenne* have the greatest number of tillers in comparisons with controls, with the lower tillers protected by the upper ones. *Phleum pratense* subjected to the lowest simulated trampling treatments also showed an increase in tillering (Bayfield 1971b). The increase in tillering capacity is a morphological response to trampling. If trampling impacts increase beyond a key threshold level, then some species such as *Holcus lanatus* lose this response. Heavy trampling causes an increase in the relative number of tillers in *Lolium perenne* only, although the relative number of tillers in both *Poa pratensis* and *Deschampsia cespitosa* remain similar in control and trampled plants. The cushioning effects of tillers in tussock species such as *Deschampsia cespitosa* probably reduces damage because there is a positive relationship between tiller number and protection effect (Sun & Liddle 1993c). Heavy trampling is sufficient to break and bruise tillers and leaves in most other species. For example, both *Deschampsia flexuosa* and *Brachypodium sylvaticum* appear to lack the ability to stimulate tiller production in response to low levels of trampling. This suggests that only species tolerant of recurrent trampling with high resistance indices are capable of increasing their tillering capacity.

7.1.2 Variation amongst vegetation types

The four ^{Vegetation} sub-community types vary in their resistance to trampling as shown by changes in vegetation cover. By comparing the trampling intensity that causes a 50 % loss in individual species cover, *Hyacinthoides non-scripta* (deciduous) absorbs nineteen times as much damage as *Pteridium aquilinum*, about twice as much trampling as the coniferous *Hyacinthoides non-scripta* stand and approximately three times as much as *Rubus fruticosus* agg. *Hyacinthoides non-scripta* (coniferous) absorbs ten and one and a half times as much trampling ^{as} than the *Pteridium aquilinum*

and *Rubus fruticosus* agg. stands respectively. Finally, *Rubus fruticosus* agg. can withstand six times more trampling than *Pteridium aquilinum*.

7.1.2.1 *Hyacinthoides non-scripta* sub-community

7.1.2.1.1 Effects of trampling on vegetation characteristics

Trampling affects growth, primary productivity and consequently the storage of assimilates in the bulb. Unfolding leaves normally develop from initials laid down in the previous year (Blackman & Rutter 1954), but trampling clearly damages and destroys above ground biomass and leaf initials, so that the ability to produce leaves in subsequent years is arrested. Thus, the negative recovery rates one year after trampling are a function of the damage to above-ground biomass, leaf initials and the nature of the short growing season.

The geophyte life-form and basal rosette leaf arrangement has a critical role in the response of *Hyacinthoides non-scripta* to trampling. The high inherent resistance and tolerance follows general trends reported by Cole & Trull (1992) for forest species with basal leaves in whorls . The presence of the bulbs at considerable soil depths and a lack of competitors may also afford a fair degree of protection from trampling (Grabham & Packham 1983). The response of *Hyacinthoides non-scripta* to low levels of trampling also appears to be similar to the picking action of leaves and inflorescences at ground level, where the picking of flower stalks does no lasting damage to the bulb (Peace & Gilmour 1949).

7.1.2.1.2 Effects of trampling on reproductive potential

The poor response of *Hyacinthoides non-scripta* extends to a high proportion of the seeding and flowering characteristics, with a more severe impact than on the other physiognomic characteristics. The impact of a second season is cumulative and has particularly damaging consequences for reproductive viability in both *Hyacinthoides non-scripta* stands. The depleted storage assimilates in bulbs of trampled plants are

insufficient to synthesise viable scapes and inflorescences as well as produce the leafy above ground biomass. Therefore, the overall trampling tolerance is related to the destruction and subsequent lack of regeneration of biomass from the subsurface bulb. In the face of considerable biotic pressure, over-winter regeneration from seeds is the major factor in the continual persistence and maintenance of colonies of bluebells (Grabham & Packham 1983, Knight 1964, Thompson & Cox 1978). Infact, population maintenance in stands depends almost entirely on seed production (Knight 1964). Crucially in this study, seed production is the most sensitive response parameter. After one season of 200 passes, relative seed production falls to 5 % and 1.5 % in the deciduous and coniferous stands respectively. This means that undisturbed stands have between 20 (deciduous) and 67 (coniferous) times the amount of seed as areas subjected to heavy trampling (500 passes per year). Bluebells are unable to produce any seed at all after 200 passes has been administered over two successive seasons. For this reason, it can be recommended to concentrate use patterns through less sensitive areas rather than spreading access spatially over a dispersed area in order to minimise damage (see Chapter 8).

This study has highlighted the fact that the ability to recover flowering and seeding characteristics from impacts as low as 200 passes per year is extremely poor. Sites will take many years to regenerate to pre-treatment conditions. For example, after two years of recovery from one season of 200 passes, the deciduous sub-community still only has an overall seed abundance that is $1/25$ th of untrampled control lanes. The re-invasion of impacted areas is not helped by the fact that seed dispersal is ineffective (Grabham & Packham 1983).

In contrast, the rapid seed production and enormous seed banks produced by other species along trails can favour the potential to germinate in a hostile environments, with some species such as *Plantago major* able to germinate even on compacted soils (Blom 1979). The impact of hikers may even scarify seeds, and the exposure of mineral soil may provide a favourable seedbed for certain species (Kuss & Hall 1991).

7.1.2.2 *Pteridium aquilinum* sub-community

The tall stature and brittle morphology of *Pteridium aquilinum* is instrumental in explaining its extremely poor resistance to trampling. Previous studies have also recognised the intolerance of bracken to trampling. For example, Kirby (1992) stated that bracken is intolerant of trampling by livestock, and cattle may suppress its regeneration and spread. The poor resistance to one season's impact was also noted by Douglas (1989), who found that the ground vegetation of a *Pteridium aquilinum* covered bank was completely eliminated after an orienteering event, and bracken paths were widened by a third.

The extensive subsurface rhizome appears to facilitate the rapid regeneration of above ground biomass after trampling by the next growing season. Long-term trampling of two seasons has a cumulative but minor overall impact on the ability of bracken to recover from trampling. The high resilience is in accordance with Cole's (1988) suggestion that the most resilient species are those that die back every winter, with perennating buds located at or below the soil surface. Regrowth of *Pteridium aquilinum* was also noted by Burden (1970), where shoots were seen emerging from the bare ground of picnic areas three weeks after the passage of nearly 8000 people on a nature trail. The response of *Pteridium aquilinum* fronds to repeated trampling is also commented upon by Goldsmith *et al.* (1970), who found that trampling did not reduce the vigour of a *Pteridetum* vegetation type.

Pteridium aquilinum is a good indicator of stable forest sites and of some value for invertebrates, but is recognised as a weed species in forestry (Biggin 1982), is toxic to livestock and humans (Cooper-Driver 1976), is allelopathic (Gleismann 1976) and is difficult to control and manage effectively. Mature stands form virtually impenetrable thickets of tall, densely packed fronds and *Pteridium aquilinum* is extremely invasive, being able to encroach^{on} its surrounds by to 1.5 m per year. Thus, it is not recommended for screening vulnerable woodland wildflowers because competition with *Pteridium aquilinum* rhizomes restricts *Hyacinthoides non-scripta* bulb

recruitment, and the shade and smothering could also reduce recruitment to bluebell populations (Grabham & Packham 1983). In existing areas, the encroachment of fronds into new areas can be prevented by cutting in June and again five to six weeks later, or spraying with selective herbicides such as Asulam (4 lb acre⁻¹ in the third week of July) (Braid 1959 in Biggin 1982, Taylor 1983 in Goldsmith 1983a).

7.1.2.3 *Rubus fruticosus* agg. sub-community

The general response of *Rubus fruticosus* agg. is similar to that recorded for *Pteridium aquilinum*, but bramble has a marginally higher resistance to trampling. The tough, woody flexible aerial parts offer a degree of protection, and even when fully defoliated, the woody biomass is still alive and capable of regenerating leafy growth. Indeed, the production of leafy biomass in heavily trampled lanes commences several weeks after the two week cover measurements were made. Trampling impacts during autumn may severely affect vegetative colonisation, because at this time the stem apices are positively geotropic and establish contact with the soil, producing roots and a resting bud (Grime *et al.* 1988). Susceptibility may also vary with the additional biotic impact of grazing, and amongst the 386 subspecies recorded for the genus.

Rubus fruticosus agg. is probably selectively avoided by walkers because of its impenetrable robust, thorny undergrowth. By way of example, Thomas (1991) observed that stands of *Hyacinthoides non-scripta* and *Mercurialis perennis* were more readily cleared than *Rubus fruticosus* agg. in woods use for combat games. This suggests that bramble could be used in same way as brash to limit access to sensitive stands. A thick tangle of arching, spiny shoots would act as a physical deterrent and recreational buffer zone by reducing lateral path width, stand penetration and the creation of new paths. It grows best under open canopies (Rodwell 1991), so overstorey vegetation beside paths and rides could be selectively thinned to promote growth.

7.1.3 *The response of individual woodland and footpath species to trampling*

7.1.3.1 *The dynamics of plant response to trampling*

The highly negative correlation between plant resistance and the recovery rate suggests that species of high resistance are less able to recover from trampling than species of low resistance. Conversely, rapid growing species are less able to resist trampling than slow growing species. Accordingly, these results confirm Sun's (1992) deduction that species with high resistance lack the ability to recover rapidly from trampling. The slow growth rate typified by resistant species is an advantage to plants in resisting environmental stress (Higgs & James 1969). In addition, Sun & Liddle (1991) found that continual trampling toughened up plant anatomy and facilitated an increase in resistance with plant age, but a decrease in the potential to recover. Overall, a 'resistance strategy' appears to be more successful than a 'recovery strategy' in order for vegetation to tolerate recurrent levels of heavy trampling. Typical resistant strategists are listed in section 7.1.3.2.1.

Species capable of rapid vegetative reproduction flourish on the margins of established trails and include *Prunella vulgaris* and *Holcus mollis*. Intermediate levels of trampling favours short-lived annuals and perennials which possess rapid rates of growth and are prolific seed producers. The recovery from heavy trampling of *Taraxacum officinale*, *Plantago lanceolata*, *Deschampsia cespitosa* and *Plantago major* as shown by their increase in relative biomass, is especially marked over the final three measurements. This suggests that a recovery strategy is an advantage for plant survival in trampled areas when trampling is interspersed by long periods of infrequent, little or no trampling. This agrees with observations made by Sun & Liddle (1991) and Sun (1992), and explains why species such as *Taraxacum officinale* typically exploit lightly trampled trail margins. Here, the recovery strategy enables species to out-compete subordinate vegetation, whilst still being tolerant of low levels of trampling. Typical recovery strategists are listed in section 7.1.3.2.2.

The correlations between relative growth rate and relative recovery rates are positive and significant for light and heavy levels of trampling, suggesting that the ability of species to recover from trampling is positively related to high growth rates. Indeed, Grime's (1979) categorisation of species which possess high growth rates as competitive or ruderal strategists helps to explain their dominance along trails (see section 7.1.5.3). High or moderate growth rates are typical of species that utilise a recovery strategy to tolerate trampling. Therefore, trampling frequency does appear to be important in the long-term survival of species. However, the best chance of survival along exposed trails is exhibited by species that share characteristics with both strategies, e.g.: *Deschampsia cespitosa*. Intermediate strategists are listed in section 7.1.3.2.3.

In order for the biomass of impacted plants to reach the same level as controls, recovery rates need to exceed growth rates. This trait is observed in most species, but *Holcus lanatus*, *Geum urbanum* and *Ranunculus ficaria* are noticeable exceptions. Relative growth and recovery rates are negative for *Ranunculus ficaria*, so the gradual loss in the ability to recover appears to be directly related to plant senescence. Given the vernal phenology of this species, the response is hardly surprising. Sun (1992) found that highly resistant species including *Lolium perenne* have the lowest ratio's, so species of high resistance would take the longest time to reach the control biomass levels. The ratio is similarly low for *Lolium perenne* in this study, and is also low for *Poa pratensis*. It remains high in *Deschampsia cespitosa* and *Plantago major*. This further endorses the point that although both of these species are predominantly species of high resistance, a limited ability to recover infers an improvement in survival. Logically, it follows that ratio's are high for recovery strategists such as *Taraxacum officinale* and *Plantago lanceolata*.

The biomass of grass species subjected to light and heavy trampling are lower than that of control plants for all species, so although trampling increases tiller number in some species, total biomass declines, which indicates reductions in tiller length and diameter. Liddle (1973) too discovered that light trampling increased the number of

tillers compared to non-compacted areas for *Festuca rubra*, but decreased their biomass. This disagrees with Kellomaki (1973), who found that light trampling of one pass per week over eight weeks increased the biomass of a woodland field layer by a third. Generally however, biomass decreases in all other species, e.g.: curvi-linear loss in biomass in *Hyacinthoides non-scripta*.

The impact of shade on plant response to trampling is discussed in section 7.1.6.

7.1.3.2 *Classification of woodland and footpath species*

Plant species featured in this study can be sub-divided into four broad survival categories by drawing on results from Chapter's 3 and 4:

- **resistance strategists** (*class A* - highly resistant; *class B* - resistant) - slow growth rate and tolerance of continual trampling. Their resistance to trampling generally conveys that species have a limited ability to compete with tall, shade tolerant woodland species and so will not spread far into original stands
- **recovery strategists** - fast growth rate and tolerance of infrequent trampling
- **intermediate strategists** - elements of both recovery and resistance strategies
- **intolerant species**

This classification does not differentiate between the adaptations shown by typical footpath species to tolerate trampling, and the potential to tolerate trampling by non-footpath species.

Poa pratensis and *Hyacinthoides non-scripta* appear to solely utilise a resistance strategy to tolerate heavy trampling. *Deschampsia cespitosa*, *Plantago major* and *Lolium perenne* appear to mainly rely on a resistance strategy, but possess limited characteristics of recovery strategists. Species such as *Ranunculus ficaria*, *Geum urbanum* and *Holcus lanatus* are of intermediate resistance but share more characteristics with the resistance strategy than the recovery strategy. *Taraxacum officinale* and *Plantago lanceolata* utilise a recovery strategy to tolerate trampling. Finally, *Mercurialis perennis* and *Deschampsia flexuosa* are highly intolerant of trampling.

7.1.3.2.1 Resistance strategists

Class A - highly resistant

i). *Poa pratensis* and *P. annua*

The most common resistant grasses in worn areas are the mixture of *Poa annua* and *P. pratensis*. These opportunist, invasive species survive where sunlight conditions prove favourable, enabling them to tolerate wear (as indicated by the positive correlation with visitor numbers) and outcompete rival species for resources. *Poa pratensis* possesses short, tough and concave leaves, and along with *Lolium perenne*, the conduplicate stem and folded leaf section proves an excellent adaptation to resist injury. *Poa annua* and *P. pratensis* are the only species observed that are capable of flowering in trail centres, sending out stunted inflorescences.

Liddle (1975a) found that high productivity of vegetation is strongly associated with trampling tolerance, so it is not surprising that plants capable of rapid vegetative reproduction such as *Poa pratensis* are highly tolerant of trampling. Under heavy trampling stress, species such as *Poa pratensis* are able to produce a high standing crop, giving them a distinct competitive advantage over other species (Burden & Randerson 1972). It is probable that an initial rapid growth phase is important for the establishment of highly resistant species, whereupon growth rates slow and growth attains equilibrium with the trampling pressure. Miller & Miller (1976) also found that species with high resistance grew quickly, but usually had slow recovery rates.

ii). *Lolium perenne*

This study recognises that *Poa pratensis* is more resistant than *Lolium perenne*. This difference is attributed to the fact that the growing point of the former species is buried deeper in the soil, and that the plant is able to propagate using underground stolons as well as by seed. However, Streeter (1971) recognised that *Lolium perenne* was still a major constituent of disturbed turf, and was commonly found on trampled paths. The high tolerance to trampling reported in this study was also noted by Grime

et al. (1988), and it is the narrow and pliable leaves of *Lolium perenne* that impart a high leaf tensile strength (Grabherr 1983).

iii). *Plantago major*

The ability of *Plantago major* to tolerate trampling has been previously noted by many workers (e.g.: Bates 1935, Blom 1979, Goryshina 1983, Grime *et al.* 1988, Kellomaki & Saastamowen 1975, Slatter 1978). The leaf rosette and adventitious roots arise from a caudex storage organ each year, and the plant is not easily destroyed by treading because this storage organ is located just below the soil surface. The upper tough, broad leaves also protect the lower ones from damage (Bates 1935). However, high rates of competition seem to rapidly eradicate the species in untrampled areas.

Further examples from the field survey could include *Sagina procumbens* and *Juncus spp.*

Class B - resistant

i). *Geum urbanum*

Geum urbanum has moderate tolerance of both shade and trampling, and with its flexible anatomy is fairly common along woodland trail margins.

ii). *Ranunculus ficaria*

The moderate resistance of *Ranunculus ficaria* also explains its lateral distribution on path margins, with tough, flexible leaves.

iii). *Holcus lanatus*

Grime *et al.* (1988) and Beddow's (1958) report that the lax tillering and shallow roots of *Holcus lanatus* makes the species largely intolerant of trampling. This disagrees with the findings of this study, where *Holcus lanatus* is moderately tolerant of heavy trampling, and light levels of trampling do not adversely affect tiller production.

iv). *Hyacinthoides non-scripta*

The response of *Hyacinthoides non-scripta* to trampling is discussed previously in section 7.1.2.

Further examples from the field survey could include *Glechoma hederacea*, *Dactylis glomerata*, *Holcus mollis*, *Ranunculus repens* and *Primula vulgaris*.

7.1.3.2.2 Recovery strategists

i). *Taraxacum officinale*

The ability of *Taraxacum officinale* to regenerate growth is as a consequence of contractile roots pulling the apical meristem 10 to 20 cm beneath soil surface. This means that this species can rapidly recover from severe defoliation.

ii). *Plantago lanceolata*

Plantago lanceolata typically occupies an intermediate trampled zone (Chappell *et al.* 1971), and the stocky leaf rosette of *Plantago lanceolata* is an advantage in tolerating trampling (Rogova 1976). Roots penetrate deeply into soils, but distribution is also related to air-filled porosity (Noe & Blom 1981), so that it tends to occupy a less severely degraded zone than *Plantago major* in the footpath succession (Bates 1935, Davies 1938).

iii). *Pteridium aquilinum*

Although *Pteridium aquilinum* is unable to recover in the same growing season in which it suffers damage, it is classified as a recovery strategist by virtue of its ability to regenerate in the following growing season (see section 7.1.2).

A further example from the field survey could include *Prunella vulgaris*.

7.1.3.2.3 Intermediate strategists

i). *Deschampsia cespitosa*

With its resilient, tough branches *Deschampsia cespitosa* is able to tolerate intermediate levels of trampling and compete effectively for resources such as light and moisture. Willard & Marr (1970) found alpine tundra communities dominated by *Deschampsia cespitosa* were also very resilient. It is well adapted to tolerate

waterlogged soils of low air content (Dawson *et al.* 1978 in Yorks *et al.* 1997) and this probably explains its survival in along trampled trails. The tussock growth form of tough and coarse leaves impregnated with silica imparts a high resistance to trampling. This species has a cosmopolitan distribution throughout the footpath zonation but appears to favour areas of impeded drainage. The response to trampling in *Deschampsia cespitosa* may also be influenced by ecotypic differentiation, phenotypic plasticity and morphological variation within species (Grime *et al.* 1988, Leney 1974, Pearcy & Ward 1972).

ii). *Rubus fruticosus* agg.

The response of *Rubus fruticosus* agg. to trampling is discussed in section 7.1.2.

iii). *Brachypodium sylvaticum*

The moderate resistance of *Brachypodium sylvaticum* is related to the tough anatomy and creeping growth, and its tolerance of shade explains the occurrence along lightly trampled woodland trail edges.

Further examples from the field survey could include *Stellaria media*, *Rumex obtusifolius* and *Hedera helix*.

7.1.3.2.4 Intolerant species

i). *Deschampsia flexuosa*

The low resistance of *Deschampsia flexuosa* reported in this study disagrees with Burton (1974), who suggests that it is structurally resistant to trampling. However, Harrison (1981) and Grime *et al.* (1988) also deduce that constant treading retards growth and flowering, with abundance and frequency declining with increasing exposure of soil.

ii). *Teucrium scorodonia*

The poor resistance of *Teucrium scorodonia* also verifies observations by Grime *et al.* (1988), who suggest that it is excluded from heavily disturbed habitats. Factors that include tall stature, brittle morphology and a rather slow growth rate contribute to its sensitivity to trampling.

iii). *Mercurialis perennis*

Mercurialis perennis is recognised as the most vulnerable species of those tested in this study. Poor trampling tolerance is related to its adaptations to withstand continuous shade in the field layer. Its absence along trails is also related to other limiting factors. For instance, Martin (1968) showed that the species is intolerant of low oxygen concentrations and waterlogging.

iv). *Silene dioica*

Silene dioica is also extremely sensitive to trampling. Its shoots would normally elongate in spring, but trampling inhibits this process. The rapid growing basal leaf rosette, which is located close to the ground, affords little protection from treading because leaf anatomy is extremely delicate.

v). *Oxalis acetosella*

Oxalis acetosella is identified in the field survey as a typical woodland trail margin constituent. Although it responds poorly to continual trampling, it is able to occupy trail margins because it is shade tolerant and gains protection from layered dominant species above it. Shallow roots, erect scapes, a slow growth rate and an adaptation to poor irradiance are all characteristics which contribute to the poor response to trampling.

vi). *Anemone nemorosa*

Anemone nemorosa is also extremely vulnerable to even low levels of trampling, where its erect stems and shallow root system afford little protection.

Further examples from the field survey include *Urtica dioica*, *Dryopteris filix-mas*, *D. dilatata* and *Arum maculatum*.

7.1.4 The impact of recreational trampling on specific plant groups

7.1.4.1 Mosses

The proportional cover of mosses is greatest in moderate and heavily trampled areas, but species diversity is richer at the trail edge and off-trail. For example, thirteen

species inhabit the trail edge compared to just three in the trail centre during summer. The prevalence of certain species such as *Eurynchium praelongum* and *Dicranum spp.* in trail centres, and *Mnium hornum* and *Polytrichum spp.* at trail edges implies a variable tolerance of trampling. Anatomical responses to trampling shown by mosses include small size and intense branching (Goryshina 1984).

The relative resistance of mosses to trampling has been noted previously by Studlar (1980, 1983) and Cole (1987). Moss cover of *Eurynchium praelongum* does not change between trail edges and the adjoining woodland, a phenomena exhibited by other forest mosses in a study by Dale & Weaver (1974). The ability of mosses to resist trampling is probably a function of their tolerance of disturbed, exposed and unstable dynamic habitats. Here, they possess a competitive advantage over higher plants, where species can survive in cracks and fissures in the centre of trails (Dale & Weaver 1974, Parikesit *et al.* 1995).

Damage to mosses appears to be greatest during summer, which reflects the rapid drying of above ground biomass of trail species from exposure to intense insolation. The dried shoots and leaves fragment easily when trodden upon, and are covered and buried by churned soil. Some colonies are capable of tolerating current levels of use because the peak growth occurs when use levels are lower in autumn, spring and winter (Barkmann 1958 in Studlar 1983).

The range of moss growth forms also affects the ability of a species to tolerate foot traffic. For example, smooth mats of *Dicranum spp.* closely adhere to bare ground and thus gain protection from fragmentation. Indeed, *Dicranum spp.* are more resistant to trampling than most other moss species (Hoogesteger 1974 in Kellomaki & Saastamowen 1975). This growth form contrasts sharply with upright, weft species such as *Thuidium tamarascinum*, which spread rapidly in areas of little or no disturbance using prostrate and ascending shoots. Other more flexible, heavily branched creeping weft species such as *Eurynchium praelongum* and *Pleurozium schreberi* are more successful in tolerating continual wear. Although *Dicranella heteromalla* is infrequent in the surveys, Studlar (1980) suggested that it was resistant

to trampling by virtue of its short turf growth form. Species such as *Polytrichum spp.* that exhibit a tall turf growth form are more patchily distributed at the trail edge, and are generally found in continuous patches far from any disturbance. Studlar (1980) deduced that leaves of *Polytrichum commune* were torn into fragments by trampling, with only the leaf bases persisting on firmly anchored stems that suffered considerable internal damage. Therefore, changes in growth forms imply a zonation of short species on the trail to tall species located off-trail, following the trend previously described for higher plants.

7.1.4.2 *Ferns*

The fragile fronds of most ferns make them particularly vulnerable to treading, which is shown by the lower frequency and abundance of *Dryopteris filix-mas*, *D. affinis*, *D. dilatata* and *Pteridium aquilinum* (see section 7.1.2) at trailside compared to off-trail areas. Adkinson & Jackson (1996) also showed that ferns constituted an equal or lower proportion of trailside flora than off-trail. In summary, ferns are less resistant to trampling than most flowering plants and mosses.

7.1.4.3 *Grasses*

Grasses constitute a greater proportion of trail centre and trailside vegetation than they do off-trail, agreeing with similar observations by Adkinson & Jackson (1996). Thus, grasses appear to be more resistant to trampling than ferns and flowering plants, verifying general statements by Dale & Weaver (1974) and Weaver & Dale (1978). The fact that Cole (1995b) found the most resistant plants of eighteen mountain vegetation sites were cespitose or matted graminoids also supplements this conclusion.

7.1.4.4 *Monocotyledonous versus dicotyledonous species*

(mainly grasses)
Monocots appear to be more tolerant of high levels of trampling than dicots, because two out of the three species categorised as class A 'resistance strategists' are

monocotyledonous grasses. Liddle & Thyer (1986) also recognised that monocots are less sensitive than dicots in vulnerable systems. Conclusions follow Liddle's (1991) rationale that as the intensity of trampling increases, the more vulnerable dicots are reduced in number and small statured grass monocots become dominant. In general, herbaceous and woody dicotyledonous woodland species are the least tolerant of all. When based purely on the classification of individual species, the proportion of monocots gradually increases in closing proximity to the path, with a marked increase at the path centre. For example, during summer the proportion of monocot species is greatest in trail centres by constituting a third, before falling to a minimum of a tenth off-trail. Findings corroborate with a study by Liddle & Thyer (1986), who found that dicots on paths that received consistent trampling in a subtropical sclerophyllous forest completely disappeared, whereas monocot ramets survived. Based on proportional coverage estimates, the dominant cover of monocots (virtually all Graminae) in path centres indicates a superior tolerance of trampling than dicot species. Where dicots do occur in worn trails, they are represented by isolated individuals of scanty coverage. A greater tolerance of trampling by monocots was noted in other work by Jim (1987), Ingellog *et al.* (1977), Liddle & Thyer (1986) and Slatter (1978). Not all monocots are inherently resistant however. For example, upright, delicate monocot species including *Arum maculatum* and *Deschampsia flexuosa* are noticeably restricted in areas exposed to low levels of wear.

7.1.5 Plant strategies

7.1.5.1 Growth forms

In areas that receive moderate to heavy levels of trampling, plant survival is favoured in species which possess growth forms where the low position of perennating buds enable species to survive wear. These strategies are mainly found in opportunistic, grassland species that invade trails after the eradication of the original woodland flora. The three main growth forms that convey tolerance to trampling are:

i). rosette species

The tough upper, whorled, basal leaves of rosette plants such as *Taraxacum officinale* and *Plantago major* are arranged in such a way that they protect the perennating bud and lower leaves from damage. Rogova (1976) also noted that stocky woodland plants with basal rosettes suffer least from trampling. Not all rosette species are resistant to trampling, so specific growth-forms do not necessarily convey a high tolerance of trampling. For example, there is a marked difference in the vulnerability of *Plantago major*, *Silene dioica* and *Dryopteris filix-mas*, which are all rosette species.

ii). tussock and tufted species

Tussock species and those species that produce many tillers aggregated together possess high resistance and flexibility (Pryor 1985, Sun & Liddle 1993c, Willard & Marr 1970), so tufted and tussock grasses such as *Holcus lanatus*, *Deschampsia cespitosa* and *Lolium perenne* are prevalent on trails. In agreement with trends reported in this study, Naito (1969) found tufted species were most frequent in trail centres, and Sun & Liddle (1993a) found that the tussock growth form was dominant amongst species growing along trails in subtropical vegetation. However, even the most resistant tussock and tufted species are much reduced in vigour. For example, there is flattening and die-back of tussocks of *Deschampsia cespitosa*.

iii). prostrate / trailing species

Prostrate and trailing growth forms are abundant in plants occurring over the range of wear classes, but particularly in trampled areas. A scrambling, branched growth form favours survival in worn areas, although to a lesser extent than the rosette and tussock / tufted growth forms. Some prostrate, clinging species such as *Galium aparine* are less durable, and are rapidly eradicated by trampling.

Other growth forms are more sensitive to trampling. Vegetation dominated by upright herbaceous and woody vegetation is spectacularly more abundant in trailside and off-trail areas than trail centres. Under low levels of trampling at trail margins, these species are generally not suppressed to the point of exclusion. Such growth forms are

typical of native woodland vegetation, with the field layer consisting of delicate, tall statured and shade tolerant plants with their apical buds held well above the ground. The two growth forms appear advantageous for species to exploit highly competitive niches where availability of light is the main limiting factor.

i). erect herbaceous species

Typical examples include *Mercurialis perennis* and *Chamaenerion angustifolium*. Erect herbaceous species are profoundly intolerant of even slight levels of trampling, corroborating Cole's (1995b) observation that erect forbs were the least tolerant growth forms in mountain vegetation.

ii). upright woody species

Changes in the relative frequency of upright woody species are less acute, and plants with woody stems and runners such as *Rubus fruticosus* agg. and *Hedera helix* can tolerate light trampling. Prickles and thorns adorning stems and shoots of the former species may also benefit survival along trails as they are selectively avoided by people. However, most other woody species are largely intolerant, e.g.: *Lonicera periclymenum* and immature tree saplings or seedlings in their first year of growth. The low survival rate amongst the latter group is because of the exposed aerial position of their perennating tissues (Hammitt & Cole 1987). The presence of woody species that are intolerant of trampling and have a reduced abundance off-trail compared to trailside may suggest a lack of ability to compete with dominant species off-trail. Delayed damage to some woody species from trampling can continue through the anticipated over-winter recovery period as a result of increased frost damage and a loss of carbohydrate reserves (Cole 1987).

7.1.5.2 Life forms

Hemicryptophyte plants with leaves in a basal rosette or semi-rosette have the highest representation in zones of trail influence, so these life-forms appear to be advantageous in the ability of species to resist and recover from trampling. Slatter (1978) also found a similar preponderance of semi-rosette and rosette

hemicryptophytes on sand dune tracks. In this study, there is a change in the life-form spectra in trampled areas that favours progressively smaller life-forms whose ability to tolerate and recover is to the position and thus degree of protection of perennating tissues. This ultimately influences the regeneration of damaged aboveground biomass in a zone where plant recuperation is normally arrested. In agreement, Liddle & Grieg-Smith (1975b) also showed that semi-rosette and rosette hemicryptophytes have a greater representation on sand-dune tracks and paths than protohemicryptophytes.

The proportion of therophytes varies with the season, ranging from being absent from heavily trampled trail centres, to increasing with decreasing trampling in summer and autumn and to being constant over all wear classes during spring. Others have recognised that therophytes are usually tolerant of trampled areas, with a shift towards annuals in trails from perennials off-trail. For example, Andersen (1995) noted that the proportion of therophytes decreased significantly from trampled areas to undisturbed areas in a variety of coastal habitats.

Geophytes and phanerophytes life-forms are generally sensitive to trampling because their relative abundance increases from trail areas to off-trail areas. Hall & Kuss (1989) also showed that phanerophytes were susceptible to impacts, and Anderson (1995) noted a similar increase in the proportion of geophytes from trampled to control sites. The ability of geophytes to recover from damage is favourable in some rhizome species such as *Pteridium aquilinum* where the underground food reserve conveys an advantage over shallow rooted species. Other geophytes are less able to recover from trampling, e.g.: *Hyacinthoides non-scripta*. Even so, trampling impacts will affect the underground storage organs of all species to considerable below ground soil depths. During spring, the abundance of vernal species even in trampled areas are dominated by a high proportion of geophytes. As summer approaches, spring specialists such as *Anemone nemorosa* and *Ranunculus ficaria* complete their life-cycles and are replaced by a profusion of hemicryptophytes and therophytes.

Upright protohemicryptophytes and chamaephytes are affected by trampling to a lesser extent than phanerophytes and geophytes, and are generally absent from trail centres. In another woodland study, Cole (1995b) deduced that chamaephytes were much less able to withstand a complete cycle of damage and recovery than other life-forms.

7.1.5.3 C-S-R strategists

During spring and summer, heavily and moderately trampled areas are dominated by:

- i). ruderals (e.g.: *Poa annua*, *P. pratensis* and *Stellaria media*)
- ii). competitive ruderals (e.g.: *Rumex obtusifolius*)
- iii). permutations of C-S-R strategists (e.g.: *Plantago major* and *Taraxacum officinale* which are both ruderal / C-S-R intermediates)

Invasive, weedy ruderal plants and their various permutations prevail at trail centres and margins where the frequent and severe disturbance of trampling creates conditions of high disturbance in environments of low stress. The ready establishment of subordinate ruderals in such areas is due to the reduced competition from neighbouring canopies and roots, high seedling relative growth rate and an early onset of reproduction (Grime *et al.* 1988, Hobbs & Huenneke 1992). High environmental disturbance reduces the competitive constraints imposed by the intolerant native taxa and bestows a competitive edge to trail flora. Few ruderal species can extend far into forest stands because the stability of woodland mitigates against this strategy (Packham & Cohn 1990). The ruderal strategy is not convivial to survival in these undisturbed, yet highly stressed environments where success is associated with very conservative patterns of resource utilisation (Grime *et al.* 1988). The invasion of ruderals will only occur when gaps are created in open canopy habitats.

The plant strategies exhibited by lightly trampled trail margin and untrampled off-trail vegetation are similar. Lightly trampled zones are frequented by:

- i). stress tolerant competitors (e.g.: *Hedera helix* and *Brachypodium sylvaticum*)
- ii). competitive ruderals (e.g.: *Circaea lutetiana* and *Galium aparine*)

- iii). C-S-R strategists (e.g.: *Glechoma hederacea*, *Silene dioica* and *Oxalis acetosella*)

Undisturbed areas are dominated by:

- i). competitors (e.g.: *Pteridium aquilinum* and *Urtica dioica*)
- ii). competitive ruderals (e.g.: *Anthriscus sylvestris* and *Lapsana communis*)
- iii). C-S-R strategists (e.g.: *Hyacinthoides non-scripta* and *Digitalis purpurea*)
- iv). stress tolerant competitors (e.g.: *Rubus fruticosus* agg., *Dryopteris filix-mas* and *Mercurialis perennis*)

The high proportion of stress tolerator plants in both zones reflects sub-communities dominated by a wide range species. The fact that undisturbed areas are dominated by competitors is a function of the spatial heterogeneity of the woodland habitat, where conditions of low stress *and* low disturbance are found. Such competitive species are able to monopolise resource capture in productive, relatively undisturbed environments by virtue of their tall stature, tolerance of impoverished light climates, growth by vigorous above and below ground lateral spread, regeneration from underground storage organs and high degree of morphological plasticity (Grime *et al.* 1988).

7.1.6 Factors that control sub-community vulnerability

7.1.6.1 Canopy density

The overall impact of trampling in all woodland communities is exacerbated by microclimatic changes under the canopy, with shaded vegetation more susceptible to trampling than vegetation growing in open or partially shady conditions. As irradiance is generally the most limiting factor operating on the woodland field layer (Packham & Cohn 1990), conditions of severe stress imparted by shade from the overstorey occur in an environment of low disturbance. Thus, many of the shade tolerant species adapted to low light levels are not simultaneously adapted to micro-environmental conditions imposed by trail use. Indeed, shade tolerant vegetation is

prone to structural breakage from a high amount of conductive and supportive tissue, large, broad leaves, thin cuticles and cell walls, large cells, poor structural flexibility and brittle morphology (section 7.1.1.4, Cole 1979, Yorks *et al.* 1997).

The relative growth rates of shade intolerant (e.g.: *Plantago major*) and partial shade tolerant (e.g.: *Silene dioica*) species growing in closed shady conditions are significantly reduced compared to their growth in open conditions. This has consequences for the long-term ability of these species to survive in stressed environments. Although the nature of response is similar and non-significant in terms of resistance to and recovery from trampling, resistance and tolerance of vegetation tends to increase as canopy cover decreases. Indeed, the heavily shaded *Hyacinthoides non-scripta* sub-community is less resistant and tolerant and path creation is more obvious than the partially shaded stand. This implies variation in vulnerability within the same species, but changes may also be a function of the ^{habitat} differences between deciduous and coniferous habitats. Conclusions agree with the findings of Cole (1993), who showed that the open areas of four vegetation types were more resistant and tolerant than shady forested areas. Rates of deterioration are also markedly more rapid in shaded vegetation, which is related to the nature of the original biomass.

Trampling in shaded coniferous woodlands significantly reduces the ability of *Hyacinthoides non-scripta* to produce viable seed counts when compared to partially shaded deciduous woodlands. As a consequence, stands of small population size present under dense shade cast by conifer plantations, but also ~~cluttered~~ stands of other mature trees and senile coppice will be more susceptible to impacts than those stands of a high population size growing in open woodland rides and glades.

7.1.6.2 *Timing of treatments*

The response of *Hyacinthoides non-scripta* to experimental trampling suggests that there is little difference between trampling all at once and administering treatments over a few months. This agrees with conclusions by Bayfield (1979a), Cole (1985)

and Cole & Bayfield (1993), but disagrees with several reports that have remonstrated that concentrating the number of passes at one time is less damaging (e.g.: Singer 1971, Landals & Scotter 1973, 1974, Nagy & Scotter 1974). However, this study acknowledges that trampling carried out over a longer duration is slightly more damaging in terms of vegetation cover, although differences are not statistically significant. In contrast, impacts directly after trampling are significantly more severe from short-duration trampling compared to long-duration trampling with regard to vegetation height.

Trampling impacts are more damaging to growth the earlier they occur in a plants life-cycle. For instance, damage to the growth and storage of assimilates from trampling in *Hyacinthoides non-scripta* is greater the earlier the damage occurs (Blackman & Rutter 1950). In this study, *Hyacinthoides non-scripta* is most sensitive in early spring, when above-ground parts have low structural resistance and when energy reserves are low. Nevertheless, the response to heavy impacts of 50 passes per week started in early spring and applied over ten weeks does not differ significantly from the response to 500 passes applied all at once in mid-spring. It is likely that if treatments were concentrated when shoots first appear and not spread over several months, or if levels of trampling were higher, then the rate of cover loss would have been much more rapid.

In terms of damage to vegetation, at high trampling intensities the frequency of trampling appears to be irrelevant, but at low levels of trampling frequency may make a difference (Cole 1985). Irrespective of frequency, continual trampling will reduce the time available for vegetation to recover, causing cover to decline indefinitely. The intensity of trampling, vegetation type and local differences in species composition are considered by Cole (1985) to be more significant factors than periodicity of trampling.

7.1.6.3 *Other limiting factors*

- i). seasonality

Survival rates of trampled vegetation are more favourable in the middle of the growing season (e.g.: early summer) than late in the growing season (e.g.: autumn). Damage to soils and trails is of more concern during the wettest months than at other times.

ii). weight of walker and stride pattern

iii). type of footwear

The type of footwear worn by walkers is likely to affect the degree of impact. For example, people wearing lug-soled boots cause significantly greater damage to vegetation cover and height than people wearing running shoes (Cole 1995c).

iv). mixed and single species sub-communities

Resistance and tolerance indices are slightly higher in mixed sub-communities than for single species stands, suggesting that mixed communities are more resistant to trampling. The homogeneous nature of the above ground biomass of species such as *Hyacinthoides non-scripta* and layering from *Rubus fruticosus* agg. may also cushion surrounding vegetation from damage.

v). Sources of error associated with experimental methodology

In woodlands used for recreation, trampling is often prolonged, of variable intensity, erratic, random, is influenced by seasonal weather patterns and micro-climatic variation and results from a variety of agents that are more, less or equally as damaging as walking. Accordingly, it is unlikely that controlled trampling experiments accurately simulated all the impacts normally associated with 'real' trampling. Indeed, it is recognisably difficult to control the magnitude of trampling impulse so that it corresponds to that of 'real' trampling (Kellomaki & Saastamowen 1975). However, it is likely that the experimental protocols are at least representative of the extents of trampling damage normally encountered in woodland sites.

7.1.7 *Estimates of stand-type carrying capacity using physiognomic features*

It is possible to estimate acceptable levels of trampling that preserve the ecological integrity of stand types investigated in Chapter 3. Approximations of carrying capacity are generated by quantifying:

- i). the amount of trampling (in number of passes per year) that creates a noticeable path
- ii). the amount of trampling (in number of passes per year) that causes paths to remain noticeable after a year of recovery

The amount of trampling that leaves an evident path is a significant threshold of impact, and the development of visually intrusive trails will help to attract, concentrate and encourage recreational use (Cole 1993). The most obvious evidence of a developing path through vegetation is the visible reduction in height, which is particularly prevalent in ground flora dominated by tall statured species such as *Pteridium aquilinum*. Yet where vegetation has grown to an imposing height it can provide a substantial barrier to people and discourage the dispersal of activities off-trail, with overgrowing fronds of undisturbed vegetation hiding the visual evidence of newly created narrow tracks.

Evident trails in the *Pteridium aquilinum* stand are caused by less than 25 passes in the first season, and after just 5 passes in the second. Cole (1993) also found that evident paths were created by 25 passes in a subalpine fern community. In the remaining vegetation types, 75 passes is sufficient to create a visually evident path. One year later, evident paths are apparent in heavily trampled 500 pass lanes for the *Pteridium aquilinum* and *Rubus fruticosus* agg. stands, and after 75 and 200 passes for the coniferous and deciduous forested *Hyacinthoides non-scripta* stands respectively. Two years later, evident paths are still apparent on the 500 pass lane for the deciduous *Hyacinthoides non-scripta* stand.

To keep paths from developing in subsequent years, recreational use along woodland trails should be kept below the ecological carrying capacity's given in Table 7.1.

Table 7.1 - The carrying capacity of woodland ground flora for recreation.

Sub-community dominant species	Carrying capacity (people per year ^a)
<i>Pteridium aquilinum</i>	100 - 150
<i>Hyacinthoides non-scripta</i> partial deciduous cover	75 - 100 ^b
closed coniferous cover	50 - 75 ^b
<i>Rubus fruticosus</i> agg.	100 - 150

^a - assuming one person makes one walking pass

^b - if ecological carrying capacity is based on damage to flower and seed parameters, then the carrying capacity for both stands is less than 25 passes per year

Estimates compare favourably with those given by Kardell (1974) for forest areas exposed to orienteering events in Sweden. Carrying capacity's were estimated at below 50 people per year for lichen-rich forests and below 125 to 150 people per year for moss-rich forests (Kardell 1974). If the ecological carrying capacity is based on seeding and flowering characteristics for *Hyacinthoides non-scripta* stands, then carrying capacity's are much lower; recreational use should be prevented at all costs, or kept below just 25 passes per year for both stand types.

Finally, Cole (1985) showed that one night of camping by three people generates 4000 steps in 100 square feet, so that each 0.214 m² of ground is trampled 87 times. This rough estimate induces a threshold level that is at or above the carrying capacity detailed for all the vegetation types. Therefore, even if vegetation types are present on the periphery of campsites, impacts are likely to be substantial.

7.1.8 Conclusions

The relationship between vegetation with environmental and soil parameters are summarised in the ecological model presented in part four of this chapter (Fig. 7.4). In summary:

- Recreational trampling is the main factor that accounts for vegetation differentiation along woodland trails, and visitor numbers is the single most important organisational gradient operating on vegetation.
- Trampling causes losses in ^{vegetation} ~~sub~~-community and species number and diversity, cover, biomass, height and leaf and stem morphological characteristics. Low levels of trampling are sufficient to severely subdue the ability of vegetation to induce flowers and seeds.
- Abundance and composition of vegetation changes from trampled trails to undisturbed shady areas. Some taxa increase, others decrease and other remain unchanged. Trail centres are typically characterised by secondary monocotyledonous plant associations at equilibrium with the trampling pressure. The richest species diversity is encountered at trail margins, suggesting that some form of disturbance maintains a diverse and dynamic plant community.
- The relationships between vegetation characteristics and trampling intensity are generally curvi-linear. This means that deterioration is most pronounced and rapid at the initial stages when trampling impacts are low, and proceeds more slowly at high levels of trampling. Rates of deterioration of the greatest magnitude occur in the first season of trampling, although cumulative damage is caused by two seasons. General responses are in agreement with work in woodlands outside of Britain by Cole (1985, 1987, 1988, 1995a), Dale & Weaver (1974), Kellomaki (1973) and Kellomaki & Saastamowen (1975).
- The nature of the response of all four woodland ground flora sub-communities to trampling is similar. Field layer vegetation that are least able to withstand a complete cycle of damage and recovery are those types that recover least (e.g.: *Hyacinthoides non-scripta*), rather than those which suffer the highest initial damage (e.g.: *Pteridium aquilinum*). This agrees with the general response of woodland vegetation in US forests (Cole 1995a). The most damaged vegetation types also show the greatest proportional recovery.

- The net result of trampling is direct injury to plants by initial impacts of shaking, touching or bending. Further physical abrasion causes the breaking and bruising of living tissue, with a reduction in photosynthetic capacity as leaf surface areas are reduced by defoliation, and thus a reduction in growth rates and recovery rates. Continual trampling stunts plants, causing them to become wilted, and many present along trails fail to flower. There are also indirect morphological responses exhibited by certain plants stimulated by low levels of trampling, e.g.: microphyllous leaves and the growth of plant tillers in certain grass species.
- It is concluded that the following are disadvantageous in the ability of vegetation to tolerate trampling:
 - brittle morphology (e.g.: *Silene dioica*, *Teucrium scorodonia*, *Urtica dioica*, *Arum maculatum* and *Oxalis acetosella*)
 - poor flexibility of leaves, stems and tillers (e.g.: *Pteridium aquilinum*, *Dryopteris* spp. and *Chamaenerion angustifolium*)
 - large, wide leaves (e.g.: *Mercurialis perennis*, *Digitalis purpurea*, *Hyacinthoides non-scripta* and *Arctium minus*)

However, damage will be offset by leaf and stem characteristics such as:

- small size (e.g.: *Stellaria media* and *Sagina procumbens*)
- flexibility (e.g.: *Ranunculus ficaria*, *Rubus fruticosus* agg., *Geum urbanum* , *Taraxacum officinale* and *Viola riviniana*)
- toughness (e.g.: *Deschampsia cespitosa*, *Lolium perenne*, *Plantago major* and *Juncus* spp.)
- ability to produce cushioning tillers (e.g.: *Lolium perenne* and *Deschampsia cespitosa*)
- Species that are tolerant of trampling are quantified by their strategy to tolerate trampling. The three strategies are:
 - resistance

resistance strategists are able to tolerate more frequent and more intensive trampling to a much greater extent than recovery strategists, which explains their persistence in trail centres.

- recovery

the facets of recovery strategists suggest that they optimally occupy a peripheral edge zone in the footpath zonation where trampling thresholds are lower. Here, their ability to grow rapidly to counter inter-specific competition and their moderate resistance facilitates optimal ecological fitness.

- intermediate

intermediate strategists share characteristics of both resistance and recovery strategists.

- The response of individual species is closely related to their morphological characteristics:

- growth form

tall, large leafed, branched herbaceous plants are generally less tolerant of trampling than low lying, rosette plants or tufted and tussock graminoids.

- life-forms

rosette and semi-rosette hemicryptophytes are the most resistant and protohemicryptophytes and chamaephytes the least.

- C-S-R strategy

ruderal are most frequent in trampled areas, whilst competitors and stress tolerant competitors are common along trail margins and in undisturbed vegetation.

- The higher the degree of protection for overwintering vegetative buds or stem apices, then the greater the chances of survival under continual trampling.

- Species typical of undisturbed woodland stands are generally highly intolerant of trampling but tolerant of shade. Conclusions drawn from Chapter 3 and Cole

(1993) indicate that the ability of common woodland species to tolerate frequent trampling is more a function of the ability to recover from trampling, rather than to resist.

- The morphology of shade tolerant species increases vulnerability to trampling. The additional stress of continuous shade reduces growth rates and thus the ability of shade intolerant species or species tolerant of intermediate levels of shade to resist and recover from trampling in shady conditions. Therefore, species that are typical of shaded vegetation are more vulnerable to trampling than species of open or partial cover microclimates. However, direct sunlight does not confer greater vegetation durability. Rather, it is the morphological characteristics beneficial for growth in light impoverished stressed environments that helps to explain the trend of high vulnerability amongst shade tolerant woodland species. Thus, patterns of change caused by trampling are always determined by the nature of the original environment.
- The carrying capacity of vegetation for recreation is much lower than previously thought (see Table 7.1). Ecological carrying capacity varies from 100 to 150 people per year in *Rubus fruticosus* agg. and *Pteridium aquilinum* dominated stands, to 50 to 75 people per year in the heavily shaded coniferous *Hyacinthoides non-scripta* dominated stand. If based on reproductive characteristics in both bluebell stands, then the permitted carrying capacity is just 25 people per year.

Chapter 7

PART TWO

**The impact of recreational trampling on woodland
soils and environmental factors**

7.2 Discussion

The second part of the discussion examines the impact of trampling on soil by pooling results from the field survey (Chapter 2), the experimental trampling trials (Chapter 3) and the main soils investigation (Chapter 5). Before detailing the response to recreational use of woodland trail conditions and soil parameters, changes in visitor numbers are examined.

7.2.1 *Variations in visitor numbers*

Across all seasons, the visitor pressure is concentrated in trail centres, before declining with distance from the trailhead. The annual number of people visiting all the study woodlands are sufficient to keep existing trails open, create unwanted paths and negatively impact upon edaphic and vegetation parameters. During summer, visitor numbers comprise 43 % of the total number of visitors recorded throughout the entire year, and use is also high in autumn (32 %), low in spring (16 %) and very low during winter (9 %). The estimates of seasonal use patterns shown (57 % use during winter, spring and autumn to 43 % in summer) are close to a ratio provided by Scott & Kirkpatrick (1994).

Recreational use varies in intensity amongst the woodland sites, with patterns of attendance influenced by season of the year, day of the week and time of day. The variation in visitor numbers between seasons is also strongly related to weather conditions (temperature, sunshine and rain). Counts in other surveys on typical weekdays have been considerably lower than at weekends or bank holidays (Schofield 1972, Burton 1974, Rogova 1976). Visitor counts in this study also peak during weekends, bank holidays and school holidays, so social trends are also responsible for variations in attendance. In any typical day, the use of woodlands is mainly concentrated in early to mid-afternoon by local visitor clientele, dog walkers, students and workers on their lunch hour. Sharp increases in visitor numbers are also experienced as a consequence of formal recreational activities such as nature trails, school and young offender visits and conservation work parties. Other more specific

activities also influence seasonal visitor counts. For example, the high number of visitors to Crackley Wood in autumn is probably related to a seasonal horde of ripening sweet chestnuts! Further variation in the use of the woodlands is reflected in the close proximity to housing, a high number of public access points and stands bordered by roads and residential streets.

7.2.2 Changes in trail conditions as a result of trampling

Trail use erodes surface organic horizons of soil, and leads to the exposure of bare ground along woodland trails. The extent of exposure is clearly related to seasonal visitor use patterns, and the appearance of bare ground along trail corridors should be regarded as synonymous with the early stages of soil erosion. This trend of increasing bare ground with intensifying levels of wear is widely reported in the literature (e.g.: Bayfield 1971a, Cole 1987). The relationship with trampling is so clear cut that bare ground cover can be crudely used as a surrogate measure of trampling intensity. This observation is in agreement with Dale & Weaver (1974), who had previously recognised that bare ground could serve as an index of trampling.

Evidence of erosion appears negligible along thickly vegetated trail margins, where the input of litter and mass of vegetation offsets the potential exposure of bare ground. Established trails appear to act as focal points for visitor use by helping to confine impacts to the controlled setting that they provide. Visitors keep to the main path surface because of its contrast with the path surrounds (Bayfield 1971a). Previous workers have shown that the exposure of bare ground was minimal at distances of greater than one metre from the trail edge (Dale & Weaver 1974) or one metre from the trail centre (Bayfield 1971a).

There is a substantial over-winter decrease in bare ground cover recorded in all woodland sites, so all year round visitor use thresholds are not generally sufficient to cause irreversible, widespread damage. However, localised erosion is recurrent in some areas, reflecting Cole & Marion's (1986) warning that soil exposure will be excessive on sites that have been intensively used for many years. Continual heavy

use will eventually lead to the exposure and damage of tree roots, muddiness, multiple parallel trails and the development of new, unwanted paths.

The high levels of wear along woodland paths reduces both cover and depth of accumulated plant litter. Burden (1970) also found a decrease in the amount of litter along paths in hazel and oak woods, and similar trends by other workers (e.g.: Bratton *et al.* 1982, Bright 1986, Liddle & Thyer 1986, Jim 1987). Physical damage by treading initially compacts litter layers along trails, before fragmenting, comminuting and scuffing away the decaying and dead material. Further depletion of litter cover and depth after comminution is augmented by run-off and leaching, with losses in the litter layer depths accentuating contact with soil horizons and increasing the extent of impacts.

Although trampling reduces litter layer constituents in size, volume and depth and erodes the upper 'A' horizon, the break up of soils deeper than litter layers by trampling in woodlands is negligible. There is also little apparent evidence to claim that irreversible damage is caused to the lower 'A' and upper 'B' horizons in woodland soils. Extreme erosion of the 'A' horizon along trails is not an acute problem in the woodlands studied here because of the high annual addition of litter, flat topography, thick soils, lush vegetation and high root densities which aid in binding soil.

A decrease in litter depth in trampled areas is consistent feature throughout all four seasons, with the patchy and thin litter layers of trails contrasting with the unconsolidated, deep leaf litter located off the trailhead. As undisturbed litter is a factor of up to a dozen times deeper than heavily trampled litter in summer, and the relationships with the indicators of trampling intensity are strong, leaf litter depth is clearly a sensitive indicator of increasing trampling disturbance. Litter layers are not replenished in trail centres to the same extent as trail margins and undisturbed areas because the biomass of trampled plants are significantly lower than undisturbed plants, there are fewer trees and shrubs and the litter input by patchily distributed species along trails is limited.

As litter is critical for efficient incorporation of organic matter and moisture retention properties in the soil (Dunn 1984), the removal of litter horizons is one factor that may explain poor regeneration of vegetation. Soil fertility is related to organic matter content (Kuss 1986), so compacted soils have low nutrient availability with recognised nutrient shortages. The subsequent loss of a transient nutrient reserve in the centre of trails will disrupt nutrient cycling, with reductions in capital and turnover rates and ultimately site fertility (Liddle & Thyer 1986, Jim 1987).

Sites of high fertility generally have a greater resistance to trampling than sites of low fertility (Del Moral 1979, Kellomaki & Saastamowen 1975, Liddle 1975b), but Sun & Liddle (1993^a) argue that soil fertility will have little effect on plant resistance to trampling. This is because many plant species that possess the anatomical and structural modifications necessary to tolerate the impacts of trampling are also largely tolerant of infertile soils. Such species are adapted to nutrient deficient soils by virtue of their inherently slow growth rates. That said, some trampled areas can have higher nutrient contents than adjacent unused areas by enrichment from animal excrement, deposition from precipitation, retarded leaching rates and powdered litter (Davies 1938, Holmes & Dobson 1976, Liddle & Chitty 1981, Speight 1973).

There are high levels of insolation along exposed trails in all seasons, especially during summer. Adkinson & Jackson (1996) also report an increase in light intensity along exposed trails in summer. Thus, path microclimates are markedly drier in all seasons apart from winter, which is due to high soil temperatures, increased evaporation rates and a lack of overstorey layers (Liddle & Moore 1974, Willard & Marr 1971).

Bruised vegetation growing on dry, baked trails is quickly desiccated by the strong sun during the summer months, so many of the surviving species are adapted to withstand conditions of temporary drought. Increased light availability at trail edges relative to undisturbed shady areas and comparatively low levels of disturbance are factors that help to account for a high species diversity and abundance at trailside.

Other attributable factors are high amounts of rainfall, minimal competition with tree roots and increases in fertilisation from the input of animal manure and urine.

7.2.3 *Changes in soil characteristics as a result of trampling*

Soil is more heavily compacted along woodland trail centres compared to trail margins and undisturbed areas. Increasing compaction as a consequence of intensifying levels of use was also recorded by Weaver & Dale (1978). These results indicate that soil hardness increases proportionally with the degree of wear, and is closely related to seasonal visitor use patterns. Across the range of wear classes, soil penetrative resistance increases rapidly at low levels of use and more slowly at high levels, reaching an upper threshold level beyond which further compaction is negligible. This response infers that a curvi-linear relationship exists between trampling intensity and the degree of compaction.

Evidence of elevated compaction levels along trails where organic layers have been denuded to expose upper soil layers suggests that mineral soils are compacted to a greater extent than organic soils. The greater levels of compaction on existing trails in the field survey compared to soils compacted over several seasons in the experimental trampling indicates that the highest levels of compaction are caused by continuous use over long periods of time.

In the winter, compaction levels in the moderately trampled zones are marginally higher than those recorded in heavily trampled zones. This is as a direct consequence of trail centres suffering temporary waterlogging, with walkers selectively avoiding these areas by spreading laterally into the less muddy trail margins. Although not examined in this study, the lateral spread of visitors on paths in winter will probably also induce an increase in track width, which was noted for paths by Lance *et al.* (1989) and Bayfield & Lloyd (1973).

Trampled soils provide a hostile environment for the maintenance and invasion of vegetation. As high levels of compaction reduce and eventually eradicates vegetation, it is assumed that establishment and germination on compacted soils is limited.

However, the substantial over winter reduction in soil compaction levels from the summer maximum reported in Chapters 2, 3 and 5 agrees with trends reported by Cole (1987). As the amount of recovery is greatest in heavily and moderately trampled wear classes, it is roughly proportional to the degree of compaction.

Heavily trampled soils are twice as dense as undisturbed soils, a difference higher than any reported in previous literature (e.g.: Legg & Schneider 1977, Ingellog *et al* 1977, Thorud & Frissell 1976). Accordingly, bulk density can be used as an index of soil compaction and thus as a reliable surrogate measurement. The bulk density of heavily compacted sandy-loam and clay-loam surface soils in this study are on average 0.50 g cm^{-3} higher than undisturbed soils. This compares with other bulk density increases of 0.16 to 0.37 g cm^{-3} in sand and sandy loams (Lutz 1945, Thorud & Frissell 1976), 0.2 to 0.6 g cm^{-3} in sandy loams (Legg & Schneider 1977, Weaver & Dale 1978), and 0.68 g cm^{-3} in gravelly sandy loams (Dotzchenko *et al.* 1967). The huge difference in soil density is a reflection of the high organic increment of undisturbed humic soils which induce low, natural bulk densities. Surface soil bulk densities of soils subjected to moderate levels of trampling during winter imply that drainage problems will be apparent at bulk densities of 1.22 g cm^{-3} or greater.

Total pore volume of undisturbed surface soils decreases by approximately a third from undisturbed soils to the trail centre. Even light amounts of wear induces a rapid reduction of 26 % in total porosity in surface soils compared to heavily compacted trail centres. In previous work, Ingellog *et al.* (1977) found that the pore volume was 15 % lower at the 0 to 5 cm depth, and Lutz (1945) gave declines of 21 % and 23 % in pore volume in sandy and sandy-loam soils respectively. In all cases throughout the study, the total porosity is greater in topsoils than subsoils in unused areas, but in compacted areas pore volumes are similar and so irrespective of profile depth. This suggests that the proportion of macropores in fine or heavy soils, which are low in subsoils anyway, are vastly reduced by trampling. When total pore space decreases below 40 % a rapid decline in hydraulic conductivity occurs (Dunn 1984). This means

that most of the moderately and heavily trampled woodland surface soils during summer, spring and autumn suffer from limited hydraulic conductivity.

Air-filled pores are physically obliterated by the physical forces of treading; heavily trampled soils have approximately one quarter of the air-filled porosity of control areas. This is in accordance with the Duggeli's (1937) assumption that trampled forest soils show less than half the air content of undisturbed soils. Trampling decreases total pore space and the proportion of air filled pores, and thus increases the relative proportion of water filled pores so trampled soils become proportionally wetter. This corroborates conclusions by Burden (1970).

During summer, undisturbed woodland soils contain ten times the amount of air-filled pore space than heavily trampled soils do, so fluctuations in soil air are strongly related to seasonal visitor distribution. Air mass flow and oxygen diffusion are inhibited in soils that have less than 10 % air-filled pore volume (Grable & Siemer 1968), so critical soil processes will be restricted in most of the heavily and moderately trampled surface soils. The air-filled porosity of surface soils are occasionally zero in samples obtained from localised areas of surface ponding. Where run-off has collected in depressions on the path surface, these soils can be assumed to be partly or entirely anaerobic. Generally however, heavily waterlogged soils are always assumed to contain some trapped air (Rowell pers. commn 1996). The high variation in air-filled porosity in unused soils is closely associated with soil water status, with control sites recharging and losing moisture at a faster rate than trampled sites.

In summer, heavy compaction slightly increases the amount of bound water in surface soils when water is scarce, precipitation is minimal and temperatures high. The water-filled porosity of heavily compacted surface soils is on average 6 % higher than those of undisturbed soils at this time. Although the relationship of water-filled porosity with trampling is positive, it is not significant and so agrees with general trends reported by De Gouvenain (1996) and Liddle (1973). The higher amount of bound

water in compacted dry soils is probably related to an increase in the amount of capillary pore space.

In terms of gravimetric water content, undisturbed surface soils are generally moister than the trampled soils of trail centres and margins when soils are wet. This response is in accordance with trends reported by Burden & Randerson (1972), Chappell *et al.* (1971), Kuss (1986) and Liddle (1975b). The compressive forces of trampling expels water from interstices and probably facilitates high evaporation rates along exposed trails. Evaporation rates are likely to be particularly high in summer, when light intensity and soil temperatures are at a maximum. Tree shelter enables woodland soils to retain moisture efficiently because shading is at least as effective in reducing the temporary wilting of vegetation as the direct addition of water is (Rowell 1994).

All study trails show surface variability, with the areas where water has collected in the rills, gulleys and troughs formed by erosion to give temporary surface ponding, contrasting with dry, surface crusts. These result primarily because compaction of moist woodland soils reduces cohesive forces between particles, causing particulate separation and rearrangement as the surface tension disintegrates from a solid to a plastic phase. As many of the study soils have a high clay fraction, puddling is a frequent phenomenon on path surfaces. The extent of surface ponding along trails reflects the amount of structural damage inflicted on surface soils. Emergent vegetation is often buried or splattered with displaced mud from the paths surface, which may indirectly affect plant survival on trails. Even in summer, some run-off water is often perched in depressions to form temporary pools.

Once dry, the puddled areas develop a hard baked surface soil cap firmly cemented by fine organic matter. Surface caps shed water easily, providing excessive run-off into adjacent areas during subsequent periods of heavy precipitation (Meinecke 1928). The net result is that soils show a range of different mechanical properties, being plastic when wet and hard when dry.

The potential of damage to soils is doubled when soils are wet (Burton 1974), and ecosystems of high soil moisture are easily damaged by even low levels of walking

(Willard & Marr 1970). Well drained, dry soils possess high load bearing capacities and so offer a greater resistance to change than wet soils do (Kuss 1986). Thus, the soils in this study are at their most vulnerable during the winter months along trails, and all year round off-trail. Indeed, soil moisture status is consistently high across the entire range of wear classes in winter, with trampled soils as wet (Chapter 2) or slightly drier (Chapter 5) than undisturbed soils. The subtle differences between water contents measured in Chapters 2 and 5 are attributed to sampling in different years and at different depths. The proliferation of waterlogged trail centres reflects the high proportion of precipitation directly reaching the ground compared to undisturbed areas. As soil water content is related to high precipitation and low temperatures, the rates of evaporation in both trampled and untrampled areas in winter are low. Additionally, the moisture status of organic rich soils is higher than organic poor soils. Thus, the moisture status of woodland soils are regulated by climate, vegetation density, drainage patterns, soil type, height of water table and soil compaction.

The organic matter content of disturbed soil throughout the year is much reduced compared to undisturbed soils, and as the intensity of trampling increases, soil organic matter content declines. This trend was also reported in other woodland soils by other authors (e.g.: Cole 1982, 1985, 1987, 1988, Dotzchenko *et al.* 1967, Dunn 1984). Trampling appears to negatively impact upon the factors that control the amount of organic matter in soil, i.e.: annual litter input and decomposition rates (Rowell 1994). Conclusions of this work are contrary to the findings of others (e.g.: Rutherford & Scott 1979, De Gouvenain 1996, Ferrero 1991, Sun & Liddle 1993a), who claim that there is little variation in the surface organic matter content between used and undisturbed areas. In woodland ecosystems, the negative relationship between organic matter content and trampling intensity is probably a function of the huge annual biomass input shed mainly during autumn by overstorey vegetation.

High and moderate levels of treading scuffs away litter and organic matter layers, and exposes underlying mineral soils. This encourages high potential rates of erosion and weathering of surface organic matter. The reduced amount of communited fresh litter,

compacted nature of the soil, high biological activity, lack of vegetation and thin organic horizons along trails all limit the potential input of organic material back into trampled soils. In some circumstances more dead plant material occurs on paths than in untrampled areas (Sun & Liddle 1993a). Consequently, the original total biomass of plant stands will strongly influence the incorporation of organic matter into soils. As trampling also reduces the number of soil organisms, the rate of decomposition is decreased and thus turnover rates of incorporation of organic matter into the soil are slow. It is also apparent that those plant species that are least tolerant of trampling occur in soils rich in organic matter. Organic matter content is affected by both the seasonal distribution of visitors, the seasonal incorporation of organic matter into trampled soil during winter and spring, canopy cover and thus the density of potential litter input.

The pH of all surface horizons regardless of proximity to the trail network is affected by seasonality, moisture status and the biological activity of soil and litter organisms. Even so, the trend of an increase in soil pH in trampled woodland soils compared with undisturbed soils in this study occurs all year round, corroborating evidence by others (e.g.: Bates 1935, Willard & Marr 1971, Ingellog *et al* 1977, Young & Gilmore 1976). The lower soil acidity of trail and trailside soils is reflected in a reduced rate of leaching in compacted soils. Compacted humus layers retain basic cations which leach away through the porous soil profiles in undisturbed areas. The concentration of anions and high organic matter content of undisturbed soils reflects the high concentrations of humic acids derived from a larger volume of decomposing litter. Indeed, one of the main internal sources of soil acidity is from the organic acids released from vegetation, soil and plant roots (Rowell 1994).

Finally, soil type and texture also govern response. The soils of the woodland sites are mainly poorly drained, acidic medium textured sandy-loam and clay-loam soils. These soils respond poorly to high levels of trampling when wet, showing localised erosion that causes path surfaces to become muddy and uneven. The poor inherent resistance to trampling by these soil series is due to weak ped strength, high water

contents and the highly porous nature of surface soils (Beard 1984). The response of soils is unsurprising because clay and loam dominated soils are most affected by recreational use when soils are wet (Bayfield & Aitken 1992). Generally however, there will be greater compression in soils of low bulk densities, with densities decreasing systematically in order of diminishing grain size from gravels to clays (Krynine 1941). This suggests that silts, silty clays and clays will resist compaction better than gravel or sandy soils when dry, but soil surfaces comprising of a high proportion of coarse rocks and stones will generally be the least affected by recreational use (Bayfield & Aitken 1992). The nature of soil boundaries also has consequences for trail management, e.g.: periodic waterlogging at soil boundaries between Dodmoor and Shifnall series (both found at Crackley Wood).

7.2.2 Conclusions

The inter-relationships of soil and environmental parameters with each other and with vegetation are summarised in the ecological model presented in part four of this chapter (Fig. 7.4). Soil impacts of the greatest severity are mainly restricted to the upper 10 cm of soil, and so the degree of impact decreases with profile depth. The initial impact of trampling moves soil particles closer together, and induces the exposure of underlying soils at the expense of accumulated plant litter and humus layers, which are fragmented and broken up by treading. Continual wear along woodland trails compacts soils by increasing bulk density and soil penetrative resistance, thus reducing total and air-filled porosity and absorptive capacity. There is also a related decline in oxygen availability, encouraging the likely onset of anaerobic conditions.

There are clear relationships between the intensity of recreational use and most soil parameters, with a distinct curvilinear relationship with soil compaction. The net result is an increase in the extent of soil erosion, although widespread erosion is not an acute problem as most of the soils in this study have thick organic horizons and high annual litter inputs. Heavily compacted soils are particularly vulnerable when

wet, with soil churning causing a proliferation of waterlogged trails. The amount of bound water increases in dry compacted soils compared to undisturbed soils, but in moist compacted soils, water contents are reduced relative to undisturbed soils.

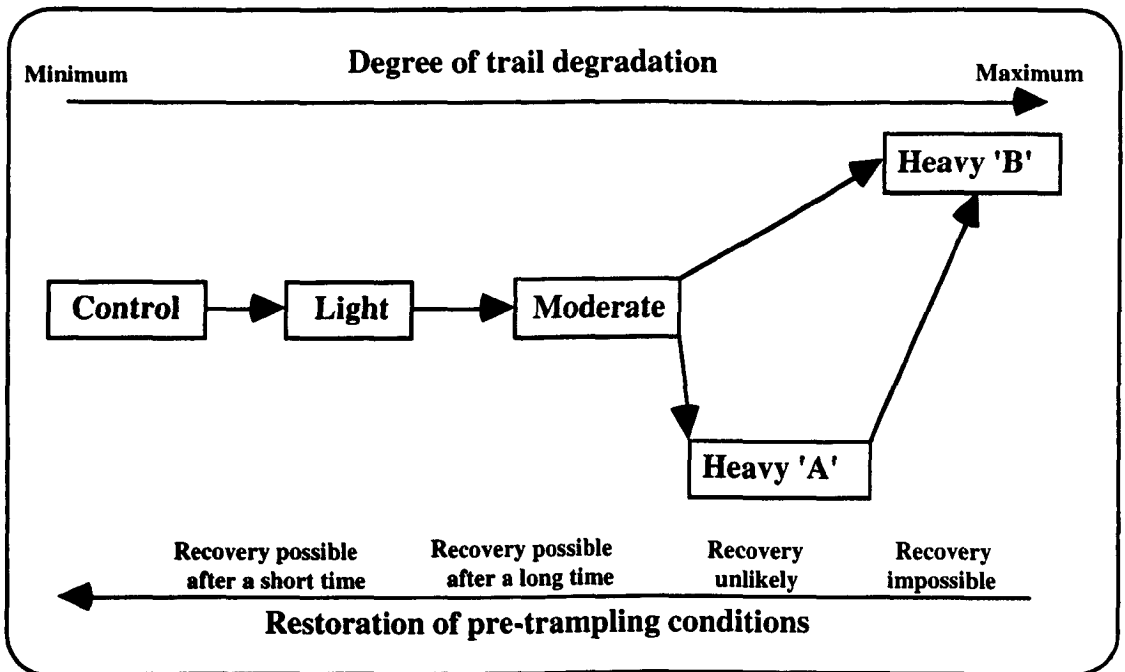
Thus, the resistance of soils to the physical impact of treading is dependent upon the moisture content, soil type and texture, extent of litter cover, soil organic matter content and micro-climatic conditions. As compaction influences soil pH and organic matter content, changes in soil chemistry and ultimately in site fertility will affect recolonisation by biota.

Two final topics of interest are open for discussion to aid interpretation of the impacts of recreational use on soils. The first is the identification of a disturbance cycle, so that the degree of soil degradation can be identified (Fig. 7.3). The second is the prediction of the likely length of time required for soils to regenerate soil structure via natural processes.

7.2.2.1 *A trampling disturbance cycle*

A simple trampling disturbance cycle based on the patterns of degradation associated with changes in the relative proportions of decaying vegetation litter, vegetation cover and bare ground exposure has been identified (Fig. 7.3). At low levels of trampling, and when litter production reaches a peak in autumn and winter, evidence of minor levels of degradation are shown by a loss in vegetation cover and litter cover. At this time, the intensity of trampling is not sufficient to completely eradicate litter cover. In control or lightly trampled areas, trampling only induces the preliminary exposure of leaf litter cover so the exposure of upper surfaces of underlying mineral soil on the trail surface is negligible. At low levels of use, the rate of conversion of the biomass of vegetation to litter is more rapid than the rates of erosive degradation of litter cover to bare ground. Similar patterns of degradation are also described as operating along trails by Bright (1986), Jim (1987) and Taylor *et al.* (1993). However, evidence suggests that soil structure is destroyed even before the eradication of vegetation and litter cover, so it is assumed that even low levels of trampling are damaging.

Fig. 7.3 - Summary of the pathways of trail degradation associated with changes to primary cover attributes in wear classes (**Control** - undisturbed; **Light** - lightly trampled; **Moderate** - moderately trampled; **Heavy 'A'** - heavily trampled, e.g.: autumn, winter, spring; **Heavy 'B'** - heavily trampled (extreme), e.g.: summer).



When visitor use is approaching a maximum in moderately trampled areas, the rate of conversion of litter to bare ground exceeds that of vegetation to litter. This leads to the exposure of bare ground cover as a direct consequence of erosional wear of leaf litter. The exposure of bare ground increases on trail centres because further inputs of fresh litter are minimal and ground vegetation regeneration is inhibited. As soil loss is initiated when 30 % or more of the ground surface is devoid of vegetation (Quinn *et al.* 1980), heavy losses in heavily and moderately trampled areas are expected. In the heavily trampled zones during summer, the peak visitor use causes the most rapid rate of bare ground exposure because the rate of conversion of litter to bare ground exceeds vegetation to litter. When use is at a minimum, the rate of conversion of vegetation to litter exceeds litter to bare ground so existing accumulated litter and additional litter input offset the rate of degradation to bare ground.

Even with these seasonal trends, an annual dynamic equilibrium is apparent between trampling pressure and the replenishment of litter horizons along trampled trails. In some areas, the annual litter input during autumn and winter is sufficient to offset the extreme exposure of bare ground suffered during periods of peak use. Two consecutive seasons of 500 passes barely expose underlying mineral soils (Chapter 3), so thick humus and organic surface soil layers inhibit the exposure of mineral soils. This suggests that soils with the thickest organic horizons are least susceptible to trampling. Indeed, the presence litter deposited along trails in winter, autumn and spring potentially cushions the upper soil layers and helps to preserve soil structure. However, the gradual erosion and thinning of organic horizons may not always be compensated by the input of organic matter from leaf fall, and so the ability to inhibit compaction and erosion diminishes with each trampling season.

7.2.2.2 *Recovery of woodland soils*

Even heavily compacted surface soils regenerate physical structure overwinter, e.g.: a mean summer bulk density of 1.51 g cm^{-3} declines to a winter mean of 1.25 g cm^{-3} . Thus, decreases in the level of soil compaction, especially at low levels, are pronounced. If soil compaction recovery rates continue at the same linear rate between one and two years recovery (Chapter 3), then it will take approximately five to six years in order for the most heavily trampled lane (500 passes) to fully recover to within 10 % of the control. However, the exact period of time will probably be much longer because rates of recovery are unlikely to be linear.

Recovery of the physical structure of soils is attributed to natural soil processes that include freezing and thawing action, the biological activity of soil organisms, wind rocking by trees and soil shrinkage and swelling by drying and re-wetting (Holmes & Marshall 1979, LaPage 1967, Lutz 1945, Kuss 1986, Rowell 1994, Thorud & Frissell 1976). It is likely that the principal agent of soil regeneration in this study is derived from wind rock and root expansion of deep rooting large standards such as *Quercus robur*. Soils are also dependent upon biological activity such as earthworm burrows

and old root channels to maintain good structure. Finally, the nature of the surveyed soils suggest that the processes of shrinking, where water evaporation causes clay particles to shrink together, and swelling, where subsequent rewetting causes swelling, could be also be important. The recovery of soils is examined in further detail in section 8.5.2.

Chapter 7

PART THREE

The impact of recreational trampling on woodland fauna

7.3 Discussion

7.3.1 *Vulnerability of woodland invertebrates to recreational trampling*

7.3.1.1 *Direct changes to macro- and mesofauna abundance and diversity*

The impoverished population density and diversity of soil mesofauna in heavily compacted areas agrees with previous observations in woodland by other workers (e.g.: Flogaitis & Blandin 1985, Ingellog *et al.* 1977, Wisdom 1988, Garay & Nataf 1982). Heavy trampling severely reduces the population density of soil and litter macro- and mesofauna by approximately 89 % in trail centres and 57 % at trail margins when compared to undisturbed zones. The degree of impact compares with Meyer's (1993) estimate of a reduction in abundance of the whole soil fauna by 70 % in heavily compacted alpine soils. Trampling levels along trail centres are sufficiently high so as to obscure the affect of seasonality on population density of all Orders, a trend that is clearly visible in undisturbed zones.

An annual recreational load of approximately 200 passes per year is sufficient to reduce total macro- and mesofauna abundance by 50 %. At this level of use, sensitive soil animal groups are rapidly eradicated. The approximation is less sensitive than Duffey's (1975) estimate for a grassland ley, where a 50 % reduction in the numbers and species of animals was caused after 120 treads per year. The most rapid deterioration occurs at low trampling intensities and proceeds more slowly at higher trampling levels, but the relationship between soil macro- and mesofauna abundance and trampling intensity are best described by a combination of linear and curvi-linear models. Even during times of peak visitor use, impoverished communities chiefly dominated by Acari and Collembola are still prevalent in heavily compacted soils and litter.

The direct deterioration associated with trampling impacts and subsequent indirect changes to habitat are best indicated by changes to the whole invertebrate community. The populations of the various mesofauna Orders show profound negative

relationships with trampling intensity, with some groups more sensitive than others. Saprophagous organisms are less affected by trampling than predatory organisms. Acari, Collembola, Coleoptera and Diptera are all found in heavily compacted trail centres, albeit impoverished in number. However, the apparent higher tolerance of trampling shown by these common and generalist groups is more of a function of the huge numbers present in woodland soil and litter rather than an adaptation to tolerate physical damage. Indeed, Acari and Collembola are the most numerous soil arthropods in respect of numbers of individuals and species (Murphy 1962), with Diptera and Coleoptera also huge groups that commonly inhabit soil and litter (Kevan 1962, Tilling 1987). The poor representation of zoophagous groups in heavily compacted zones is related to the scarcity of suitable saprophagous and microphytophagous prey items.

The significant differences found in the abundance of various Acari families between trampled and undisturbed areas in the two woodland soils agrees with work by Garay & Nataf (1982), and with observations on Oribatid mites by Ingellog *et al.* (1977) and Borcard & Matthay (1995). Small sized Acari (< 0.2 mm) are significantly more abundant in heavily compacted soil and litter than moderate and large sized Acari. These tiny Acari are able to occupy a niche that avoids both predation from predatory arthropods which are largely absent, and competition for resources with other organisms. Factors responsible for the increase in relative proportion of small sized Acari include the fact that some species of Acari can tolerate trail conditions of low soil O₂ or high soil CO₂ (Hughes 1943), and that small Acari are common in heavy clay soils of restricted pore space (Kuhnelt 1962). The patchy distribution of mites is also related to localisation of food supply and eradication of pore space. Certain species of Acari may even prefer compacted soils. Indeed, Heisler (1995) suggests that the profusion of tiny Gamasida in trampled areas is because the increase in the number of water-filled pores in compacted soils contain an abundance of their preferred prey of nematode worms.

Many Acari are predatory, but some also feed on fungal hyphae, spores, rotting leaves, faecal material and cellulose decomposing bacteria (Stalfelt 1973, Tilling 1987), and the majority of surface dwelling Collembolans are widely saprophagous and fungivorous (Poole 1959, Murphy 1962, Stalfelt 1973, Tilling 1987). The feeding habits of Acari and Collembola imply that the decline in abundance of these two groups is strongly related to the drop in microbial biomass and organic matter content in trampled areas. Fluctuations in population density are also related to availability of food items.

Heavily compacted forest soils are dominated by low numbers of small sized Collembola. Minor levels of compaction at path margins reduce Collembolan population density by over a third compared to populations present in undisturbed areas, but the decline in population density of Collembola is significant only in heavily compacted zones. This observation is in agreement with Garay & Nataf (1982), who found a reduction in numbers of Collembola in zones of high perturbation only.

The difference of 31 % in Diptera population density between path edge and undisturbed zones suggests that Dipteran larvae are one of the least sensitive groups to low levels of trampling. The ability to tolerate lightly trampled conditions probably favours species that prefer poorly drained mud. Light levels of trampling do not seem to compromise population recruitment and the abiotic conditions of path edge zones do not overtly affect Dipteran larval development. Nevertheless, densely compacted woodland soils may prevent adult emergence, limit egg laying ability, promote poor survival rates and ultimately modify the life-cycles of certain species.

Individuals of Enchytraeidae are mainly absent in trampled trails, especially when seasonal visitor use is at a minimum. Their inability to persist in trampled areas is due to an intolerance of desiccation, a lack of suitable habitat in the form of burrows in fissures and crevices and a requirement for oxygen saturated soil (Kuhnett 1962, Schaefer & Schaermann 1990). In agreement with Pearce (1984), Ingellog *et al.* (1977) and Chappell *et al.* (1971), Lumbricidae density is severely reduced in

compacted zones. However, abundance is generally low in acid soils anyway (Schaefer & Schaermann 1990), explaining their absence in the acidic mor soils of Tilehill Wood, and scarcity in the acidic mull soils of Tocil Wood.

The other groups that are extremely sensitive to trampling include Pseudoscorpionida, Araneae, Diplopoda and the majority of the Insecta Orders. Araneae appear to be a particularly sensitive Order, with an 65 % reduction in numbers between light and undisturbed zones. The vulnerability of Araneae to trampling has been recognised previously by Flogaitis & Blandin (1985) and by Duffey (1974), who found that very light trampling makes moss and lichen habitat unsuitable for the spider *Trichoptera cito*. Pseudoscorpionida, who are active predators that feed on Collembola and Psocids (Tilling 1987), are also a very sensitive group. The highest seasonal trampling intensities in summer cause the lowest population densities of Araneae and Pseudoscorpionida. In accordance with the findings of Duffey (1975), Isopoda are slightly more sensitive to trampling than Araneae. Diplopoda are identified as the most sensitive group, with their numbers decreasing by 83 % between trailside and undisturbed zones. Their absence is as a result of the avoidance of compacted soils by Diplopoda where their detritivorous food source is scarce. Wisdom (1988) also found that woodland inhabiting Diplopoda are also extremely susceptible to trampling.

In contrast, the predatory group of the Chilopoda are reduced by just a tenth between path edge and undisturbed zones. Although the exposed nature of typical path microclimates do not favour Chilopoda as they are prone to water loss (Tilling 1987), mobile and opportunist predatory Lithobiomorpha and Scolopendromorpha Chilopoda make up most of the individuals caught in trampled areas. Their mobility explains continual lateral spread from less disturbed peripheral zones. However, the soil dwelling burrowing Geophilomorpha, which favour the crumb structure of mull 'A' horizons (Schaefer & Schaermann 1990), are particularly prone to eradication by trampling. The presence of other mobile predatory invertebrates along trails, including adult Coleoptera, suggests that trampling can increase the number of species associated with bare ground, and also the proportion of scavenging species.

Although compacted surface soils will inhibit the normal vertical migration of predatory species into soil in response to the onset of unfavourable dry conditions and scarcity of food (Purvis & Curry 1980), it may actually encourage a horizontal migration to less perturbed areas.

7.3.1.2 *The effects of indirect habitat changes on mesofauna abundance and diversity*

In addition to the response to the direct impact of physical treading, indirect changes to habitats also influence mesofauna populations. Indeed, trampling invokes changes to vegetation height and cover, microclimatic modifications, comminution of litter and erosion of the 'A' horizon, soil compaction and physical and chemical soil characteristics.

The amount and distribution of pore space is critical for invertebrate survival because it determines the nature of living space and controls humidity and gaseous conditions (Murphy 1962). Compaction shapes community composition by progressively excluding larger species that inhabit large pores and interstices, as there is a clear negative relationship between trampling intensity and organism size of Acari. As soil pores are physically obliterated by heavy compressive forces, in-situ soil fauna are eradicated and colonisation back into the soil interstices is limited because compaction restricts the movement of soil animals.

In conjunction with a decrease in the abundance of the larger pore reliant fauna, the general decrease in air and water availability in trampled areas controls alterations in community populations and plant death. Soil fauna that inhabits micropore soil water must be capable of surviving temporary desiccation. Groups such as Enchytraeidae and insect larvae are largely intolerant of such conditions (Kuhnett 1962, Purvis & Curry 1981), so their continual absence in trampled path soils and litter is unsurprising. The abundance of mesofauna is reduced by dry conditions, with the minimum of development in summer occurring in tandem with conditions of low soil moisture. The reduction in size of soil animals in compacted soils may also be

exacerbated by the existence of a relationship between fauna size and the ability to resist drought (Kuhnett 1962). Water-filled pores may also act as an active competitor for living space with the soil fauna, explaining why numbers are so much reduced in waterlogged soils.

Trampling alters the composition and amount of litter, with a changes in visitor use patterns related to seasonal declines in abundance in path centres. The higher populations of soil fauna in winter and autumn is typical for a mor / moder litter type when compared to mull type because the latter profile tends to freeze in inclement weather. Indeed, the impact of frost damage on exposed trails in winter is also considered a major limiting factor.

7.3.2 *Vulnerability of woodland micro-organisms to recreational trampling*

7.3.2.1 *Direct changes to micro-organism biomass and respiration rates*

The trend of significantly higher field respiration rates and a non-significant lower microbial biomass in trampled soils compliments the findings of Duggeli (1937), Smeltzer *et al.* (1982) and Santruckova *et al.* (1993). Field respiration rates are approximately twofold higher in heavily compacted surface soils compared to undisturbed surface soils, so microbial activity reaches a maximum in compacted soils. The trend of higher respiration rates in compacted areas was also described by Santruckova *et al.* (1993). If no gaseous exchange occurs, then the duration of aerobic conditions in undisturbed soils lasts eleven times longer than conditions in heavily compacted soils.

The microbial biomass of undisturbed soils is approximately one and a half times higher than biomass recorded in heavily compacted soils, although overall differences are not significant. This ratio compares favourably with others given by Duggeli (1937) and Santruckova *et al.* (1993).

7.3.2.2 *Indirect habitat changes to micro-organism abundance*

Along with recreational trampling, factors such as soil acidity, temperature and aeration affect microbial communities. As the pH of undisturbed surface soils is lower than in trampled areas (Chapters 2 and 5), increased soil acidity reduces the microbial respiration rates of micro-organisms in undisturbed areas relative to trampled ones. This is because highly acidic conditions reduce the potential rate of organic matter decomposition and the release of mineral nitrogen (Rowell 1994).

The mass of carbon dioxide liberated from the soil is also dependent upon soil temperature, which varies diurnally, annually and with profile depth (Rowell 1994). As soil temperatures rise, the respiration rates of micro-organisms also rise and the body of respiring organisms utilise oxygen at a faster rate. This explains the greater rates along exposed trails compared to shady undisturbed areas where less sunlight, and thus heat, reaches the woodland floor. A summer maximum and winter minimum shows the impact of annual temperature fluctuations on soil respiration rates.

Changes to the microbial biomass are directly influenced by soil compaction altering the properties of gas and water exchange. This study suggests that oxygen in the air-filled pores of moist undisturbed soils can supply the needs of the biomass from between several hours to almost two days. Micro-organisms respire rapidly in compacted pores that contain a low amount of air, and so the rapid utilisation of depleted oxygen reserves can be expected. As the diffusion and mass flow of oxygen into and through the soil matrix is retarded by compaction (Dunn 1984, Grable & Siemer 1968, Legg & Schneider 1977), intensive microbial activity will enhance the onset of anaerobic conditions. Anaerobic conditions decrease the overall microbial activity, with oxygen shortages killing off nitrifying bacteria, reducing mineralisation and changing the community composition to anaerobic denitrifying bacteria (Dunn 1984, Rowell 1994, Speight 1973, Whisler *et al.* 1965). Other authors have reported a change in community composition, with nitrifying bacteria unable to survive trampling and anaerobic bacteria twice as abundant and principally dominated by denitrifying bacteria (Duggeli 1937, Speight 1973). As the majority of green plants

will uptake their nitrogen as nitrates, the activity of nitrifying bacteria biomass is vital in controlling soil fertility (Stalfelt 1973).

The soils of Tocil Wood are predominantly mull and so are principally dominated by soil bacteria (Murphy 1962). The impact of microbivory on these soil bacteria will be reduced as trampling eradicates the microbivorous organisms, although this factor is probably minor in explaining observable differences. Soil respiration rates are assumed to be proportional to the organic matter content of the soil (Puri 1950, Rowell 1994). Although the organic matter levels are lower in trampled soils than undisturbed soils (Chapters 2 and 5), litter is highly fragmented as a consequence of treading. The high litter surface area probably facilitates a rapid increase in respiration rate to such an extent that there is greater carbon dioxide output in trampled areas even though the biomass is lower. Additionally, microbial populations are less able to decompose organic matter when plant residue builds up on undisturbed soils (Rowell 1994). Puri (1950) even attributed differences in field respiration rates between bare ground and vegetated soil to vegetation immediately absorbing carbon dioxide and lowering output.

7.3.3 Conclusions

7.3.3.1 Summary

Although the findings from this study fail to differentiate between direct and indirect impacts of trampling, the overall impact has a deleterious and cumulative impact on soil fauna. The changes in soil fauna composition caused by recreational activities will ultimately have indirect consequences on soil type and soil processes, as populations have major influences over the movement of organic materials and minerals through the soil (Speight 1973). Evidence suggests that disturbance impacts help to shape edaphic fauna communities so that their structure and diversity is related to the type, intensity and frequency of impact.

Without exception, all woodland soil fauna Orders, independent of humus type, are extremely sensitive to recreational trampling. There are rapid losses in specialist species of narrow ecological niches so as trampling increases, soil and litter fauna becomes dominated by impoverished communities of progressively smaller, saprophagous, opportunist and common species. These communities are less affected by recreational use than larger, rapidly eradicated predatory zoophagous species. At upper thresholds of damage, common soil and litter fauna Orders still inhabit soil and litter, and limited populations are at a dynamic equilibrium with recreational wear that has already eradicated overlying vegetation cover.

The lightly trampled path edge zone community remains reasonably representative of the undisturbed zone community in terms of diversity. However, spatially heterogeneous trampling, especially along path margins, strongly influences the distribution and abundance of the more sensitive soil organisms groups, and will negatively impact upon survivorship and fecundity with respect to pupation and emergence times.

7.3.3.2 *Use of soil fauna as bioindicators of soil compaction*

As the equilibrium of forest ecosystems is maintained by soil activity, the use of biological indicators in the assessment of soil damage is a useful exercise for the conservation and management of woodlands (Garay & Nataf 1982). Communities of abundant arthropods provide a useful bioassay for likely environmental gradients in and around forest recreation areas (Mahoney 1976).

In this study, soil organisms are not identified beyond Order level so Acari body size is adapted to offer an alternative that is relatively easy to measure and requires little in the way of taxonomical expertise. However, it is recognised that certain groups can be spectacularly absent even when impacts are slight. Indeed, Garay & Nataf (1982) found that Brachychthoniidae are very sensitive indicators of trampled forest soils. In this study, the presence / absence of Diplopoda can be used in the same way. Three

damage indices were classified according to the relative proportions of large, moderate and small sized Acari (based on body length in 'mm') (Table 7.2).

Table 7.2 - Bioindicator index using Acari body length.

Relative proportion of Acari size categories	Level of soil compaction	Index of damage
> 67 % small (< 2 mm)	Heavily compacted	<i>Damaged</i>
> 33 % but < 66 % small (< 2 mm)	Compacted	<i>Tolerable</i>
Equal amounts of small (< 2 mm), moderate (2 to 5 mm) and large (> 5 mm)	Undisturbed	<i>Undamaged</i>

This bioindicator index varies with soil depth, type and texture, frequency and timing of visitor use patterns, seasonal population cycles, microclimate and canopy cover but not with litter type.

Chapter 7

PART FOUR

Overview of the impact of trampling on woodland vegetation, soils and soil fauna

7.4 Summary

Human disturbance impacts exert a powerful influence on vegetation and soils in semi-natural ancient deciduous woodland of Warwickshire, England. ^{urban fringe}Trampling permanently transforms impacted areas into blocks that do not resemble the original, undisturbed environment. There is a loss in species richness and the development of a specialised secondary plant association dominated by resistant grassland species. The integral ability of individual vegetation species to successfully tolerate recreational trampling is related to their morphological characteristics, growth form and life-form, ecological and regenerative strategies and environmental characteristics.

The impact of trampling on vegetation is a more precise indicator of recreational use than soil and soil fauna characteristics. Even so, vegetation composition, abundance and diversity are all influenced by a complex array of inter-correlated edaphic parameters that are modified by trampling. An ecological model was constructed to summarise these interactions (Fig. 7.4). As impacts by direct physical treading and indirect modifications to soil physical and chemical parameters cause adverse impacts on abiotic and biotic communities, soil characteristics are recognised as important in shaping forest vegetation and associated invertebrate fauna. Although changes to woodland soils induced by recreational trampling are considered to be less obvious than impacts on the biota, soils are probably more important because they are integral for subsequent plant establishment, growth, reproduction and succession.

The additional eradication of soil mesofauna and micro-organisms by trampling has dire consequences for woodland primary productivity. This is because the normal soil processes of nutrient turnover are inhibited and / or modified by changes in population size and community composition forced by recreational trampling.

Trampling is the primary factor that accounts for vegetation differentiation along trails in woodlands, and intensity of visitors represents the single most important organisational gradient operating on the vegetation. There is a noticeable shift in vegetation composition from trampled trail centres to trail edges and to undisturbed areas located off-trail, with some taxa increasing, some decreasing and others remaining unchanged. If environmental conditions are favourable, continual wearing of trails actually generates a sward that is better adapted to withstand visitor pressure and is at equilibrium with the trampling pressure. Trail taxa are dominated by a species poor sub-community of slow growing resistant strategists, which show morphological adaptations to tolerate damage, e.g.: increase in the production of tillers and small leaves. Trailside flora tends to be dominated by rapid growing competitive strategists, and is also the zone of the richest floral biodiversity.

Shade tolerant species located off-trail are least likely to survive the additional impact of trampling. Woodland plants typical of shaded stands are characterised by delicate leaves and stems, a single exposed perennating bud, and an adaptation to moist, undisturbed soils where inter-specific competition is severe. This means that tolerance to trampling is generally poor in most woodland species. This means that the ability of species such as *Pteridium aquilinum* and *Rubus fruticosus* agg. to tolerate damage is more a function of their ability to recover from damage rather than to resist. The suppression of upright herbaceous and woody phanerophyte shrubs at the periphery of sites indicates the spatial extent of trampling, and suggests that the effect of the trail corridor is narrow.

As the intensity of visitor use increases, the impact on biotic and abiotic ecosystem components grows. The curvi-linear nature of use / impact relationships allows the identification of use thresholds at the trampling load where response curves initially approach the asymptote (Cole 1987). The curvi-linear relationship identified by this study suggests that damage progresses at the most rapid rate when use levels are low. This leads to a call to manage visitor access by concentrating use in a limited number of sites, and to discourage dispersed recreational activities. The practical management

of woodlands for recreation is discussed in more detail in Chapter 8 where criteria are synthesised in a format and context that can be immediately be used by land managers to formulate management policies. An 'Index of Vulnerability' is provided (Fig. 8.1) to allow land managers to assess the potential impacts of recreation in any hypothetical woodland site. A full management checklist to resolve conflicts of recreation with conservation in woodlands and accompanying ecological model (Fig. 8.1) are also given.

The conclusions of this study provide models to estimate the carrying capacity of similar areas for recreation. They provide a quantitative basis to promote understanding of the nature of interactions between use levels, habitat characteristics and micro-climatic conditions in lowland English woodlands. The intensity of impact, frequency and intensity of use and environmental factors such as canopy density control the degree of disturbance. The potential of woodland sites for use appears to be affected by access, local population levels, soil type, woodland area and shape, proportion of open areas and vegetation type.

There is ample opportunity for recreation ecologists to follow personal interests for further research because the field is so poorly documented. One future topic for research might include defining the carrying capacity of other N.V.C woodland sub-communities, allowing different woodlands to be graded according to their overall vulnerability. However, as this study has thoroughly investigated the ecological response of vegetation, soils and soil fauna to trampling impacts, emphasis should now be placed on how to repair damaged sites (e.g.: Bayfield & Aitken 1992). Indeed, further understanding of how to restore impacted areas back to pre-damaged conditions merits considerable attention (Cole pers. commn. 1994).

By addressing the three main objectives set out in section 1.5, this study concludes that the response of vegetation to trampling in British temperate deciduous woodland is similar to the response delineated in woodland and forest types in other parts of the world. The conclusions can be extrapolated with confidence to related N.V.C

woodland community types exposed to similar level of use, and with caution to other woodland types and recreation areas such as campgrounds and picnic areas.

Chapter 8

THE MANAGEMENT OF WOODLANDS FOR RECREATION

8.1 Introduction

In order to preserve the ecological integrity of woodland sites, the number of people visiting Britain's woods will have to be controlled at or below the estimates of carrying capacity that have been determined by this study. Carrying capacities of different sub-community vegetation types and individual species vary between 25 and 150 passes per year; these are lower than impacts required to induce changes to soil fauna populations and soil parameters which means that the impact of trampling on vegetation is a more sensitive indicator of recreational use.

The management of woodlands must be designed to cope with periods of maximum recreational use, especially during summer and early autumn. This can be achieved by:

- utilising paths and rides to steer people away from sensitive areas and onto more durable vegetation types, by cordoning off sensitive stands
- encouraging maximum use on organised trails that are clearly marked and adequately surfaced
- concentrating use in impacted areas, especially in more tolerant vegetation types

It is a common misconception that if trampling is unavoidable then impacts should be spread over a dispersed area in order to limit damage to sites. Not only is the most damage caused at low recreational thresholds, but in the case of vegetation, the flowering and seeding viability of species such as *Hyacinthoides non-scripta* are threatened by even lower trampling intensities. This study indicates that the capacity of woods to accommodate free-roaming visitors is much lower than previous literature suggests, so dispersed activities such as orienteering, paintball, picnicking, nature trails and school visits should be discouraged especially in densely shaded woodlands. Vegetation loss can be reduced when use is concentrated on one site, as opposed to being distributed over several sites (Cole 1985, 1987), but a strategy of concentrating use in particular sites is only effective when use levels are low and sites are fairly resistant in the first place (Cole & Fichtler 1983).

8.2 Implications for vegetation sub-community carrying capacity and stand management

Although *Hyacinthoides non-scripta* is probably one of the most resistant ground flora species present in British temperate deciduous woodlands, most native woodland species are intolerant of trampling. However, some species do possess an ability to recover from damage, e.g.: *Rubus fruticosus* agg. and *Pteridium aquilinum*. Complementing conclusions by Cole (1993), it appears that the ability of woodland species to tolerate recurrent trampling may be more a function of an ability to recover from trampling rather than an ability to resist.

Land managers can obtain an immediate appraisal of the potential for a site to withstand recreation by the various plant strategies exhibited by species. Impacts will be greatest in tall, herbaceous and woody phanerophyte, protohemipterophyte and geophyte vegetation, which exploit shady conditions of high environmental stress and competition. Impacts will be least in short statured, rosette, tufted and tussock hemipterophyte vegetation, which thrives in the open conditions of high environmental disturbance. Shade tolerant species are the least resistant to trampling, with this group including many of the typical woodland species identified as occurring in areas of little or no trampling.

An index of vulnerability is presented in Table 8.1 for resource managers to assess the potential of woodland stands to withstand recreational use, based on dominant vegetation and environmental characteristics. The index can also be adapted for use in other non-woodland habitats. The identification and subsequent mapping of vegetation stands dominated by intolerant species allows the rapid demarcation of vulnerable areas suitable for habitat zoning. This means that specific recreational activities can be permitted in woodlands as long as small ecologically important areas are identified and protected. However, zoning must also be multi-disciplinarian in approach and take into account other characteristics, such as nesting birds, wet woodland flushes etc.

Table 8.1 - An index of vulnerability for woodland sites. Sites for evaluation are graded 2, 1 or 0 points according to ratings of each of the eleven *dominant* factors, yielding a score that ranges from zero to 22 (zero to 4 = **not vulnerable**; 5 to 9 = **intermediate**; 10 to 15 = **vulnerable**; 16 to 22 = **extremely vulnerable**).

DOMINANT FACTOR	Index of vulnerability		
	HIGH (2 points; max. 22)	MODERATE (1 point, max. 11)	LOW (0 points; max. 0)
Locality	Urban	Suburban	Rural
Light climate	Closed shade	Partial shade	Open
Soil moisture status	Wet	Dry	Moist
Typical flora	Dicots	Variable	Monocots
Vegetation stature	Tall	Intermediate	Short
Leaf morphology	Wide, large, delicate	Narrow	Flat, small, basal, tough
Stem anatomy	Brittle, rigid	Branched, layered, woody	Flexible, tussock / cespitose
Growth form	Erect herbaceous and woody	Prostrate	Rosette, tussock / tufted
Life-form^a	Phanerophytes, geophytes, chamaephytes, proto- hemicryptophytes	Therophytes, semi- rosette hemicryptophytes	Rosette hemicryptophytes
Ecological strategy^b	Competitors	C-S-R intermediates	Ruderals

^a - based on classification by Raunkiaer (1934)

^b - based on classification by Grime *et al.* (1988)

Working example: the index of vulnerability was applied to undisturbed vegetation of transect 4 in the spring survey from Tocil Wood (Chapter 2), and the stand scores as follows: suburban (1), partial shade (1), moist (0), monocots (0), intermediate (1), narrow (1), brittle (2), erect herbaceous (2), geophytes (2), C-S-R intermediates (1). The final score of 11 points implies that the stand is '**vulnerable**' to potential recreational impacts.

A major problem that confronts land managers is whether to increase vegetative productivity and thus carrying capacity at the expense of ecological diversity. Indeed, the carrying capacity can be artificially increased by manipulating the nutrient status of soils (Streeter 1971). Watering, seeding and adding fertiliser increases the resilience of semi-natural swards to trampling, with the addition of litter, faeces and urine promoting the rapid growth of trampling tolerant, nutrient loving species such as *Poa spp.* and *Lolium perenne* (Beardsley & Wagar 1971, Speight 1973).

The morphological response of increased tillering capacity shown by lightly trampled plants of *Lolium perenne* and *Deschampsia cespitosa* in this study highlights the potential of grassland species to revegetate impacted trails when environmental conditions are favourable. However, the choice of species should not only be based on plant tolerance to disturbance impacts, but should also take into account a wide range of factors pertinent to the site. For example, Goldsmith (1983a) argues that *Lolium perenne* is undesirable in conservation areas for both aesthetic and ecological reasons. Furthermore, the application of fertilisers to improve ground coverage may have other damaging effects, e.g.: ground dwelling invertebrates.

Another approach is to promote the sowing, propagation and planting of native trampling tolerant species highlighted in this study along existing eroded areas and in newly created habitats, such as urban woodlands, where the demand for recreational use is likely to be high. Woodland species capable of withstanding moderate levels of trampling such as *Geum urbanum*, *Deschampsia cespitosa*, *Hedera helix*, *Ranunculus ficaria* and *Brachypodium sylvaticum* can be considered for inclusion in seed mixtures. Trampling tolerant species will help to repair soil structure after trail closure, and can act as nursery species to facilitate plant succession back to the original flora. Certain species such as *Plantago major* have effective root penetration and are able to germinate in and on compacted soil (Blom 1979), so the colonisation of disturbed areas to restrict soil erosion is plausible. Artificial methods can also regenerate soil structure and provide a favourable medium for plant colonisation.

However, these methods, which include physical loosening by hand or machines, can also damage the rhizosphere.

The potential use of bryophytes to inhibit soil erosion is recognised in this study. Species such as *Eurynchium praelongum* and *Dicranum spp.* are fairly resistant to trampling and have the ability to regenerate freely from creeping, protected meristems and tough, wiry stems. As such, using mosses to revegetate denuded areas will consolidate and bind damaged soils, and encourage natural succession. Depending on individual habitat preferences, fragments from species should be sown directly onto suitable substrates adjacent to trails such as bare earth, logs and rocks.

Demand for recreational use of woodlands is often dependent on the nature of the sub-communities that are present. The magnet of bluebell vistas in spring encourages public access, as stands offer peace, colour and recreation to the public (Packham & Cohn 1990), and a visit to any bluebell wood in spring is an unforgettable experience (Rodwell 1991). In 1998, the addition of *Hyacinthoides non-scripta* to schedule eight of the Wildlife and Countryside Act by the Joint Nature Conservation Committee was sanctioned to outlaw the illegal trading in bluebell blooms and bulbs harvested from woodlands. The conclusions of this study suggest that this appointment is further enforced by the adverse response to trampling. In contrast to Britain's bluebell woods, woodlands dominated by dense, cluttered stands of *Rubus fruticosus agg.* and *Pteridium aquilinum* are less aesthetically pleasing, and overuse by visitors is of a lesser concern.

8.3 Implications for the carrying capacity of woodland soils and trail management

The most effective way of protecting sensitive and vulnerable woodlands is by maintaining and improving the footpaths. If users can be encouraged to walk single file on obvious tread (e.g.: by waymarking), managed paths can become the focal point of visitor use. This will avoid some popular paths becoming so badly eroded that they become obtrusive scars on the landscape. Indeed, an obvious single narrow

bare path in a large area will have a lower environmental impact than several multiple trails.

The findings of this study show that deterioration of soil physical structure is most rapid at low levels of recreational use, and between 250 and 300 visitors per year cause damage that will be difficult to reverse. The deterioration of sites is shown to reach a near maximum after just two seasons of trampling, and additional recreational use is unlikely to induce any further significant changes. Indeed, most soil physical and chemical parameters stabilise at an upper threshold level, but only if current use levels remain the same. Extreme recreational loads may cause some to reach a level of degradation where recovery is not possible.

If trail rehabilitation is to be attempted, the rest-rotation system denoted by Burden & Randerson (1972), Lutz (1945) and Thorud & Frissell (1976) is not recommended because near maximum levels of disturbance occur in the first season of trampling. Instead, the selection of trails for permanent closure should be considered. Closure can be enforced by the selective channelling of visitors into less degraded areas, bearing in mind that simple track closure may be inadequate to restore the vegetation in a reasonable timescale. The confinement of walkers onto established tracks to avoid dispersal and the use of alternative routes is also recommended to avoid localised path braiding. This leads to deliberate policies to contain users in designated areas, often relying on recreational 'honeypots' to draw visitors away from sensitive sites.

The impact of trampling is highly correlated with visitor use patterns, so trails can be blocked off at specific times of the year to aid recovery. If access is controlled in winter then the main natural agents of recovery will not be affected. Tree felling should be discouraged and tree planting encouraged near heavily impacted trails. Large standards provide valuable leaf litter to help maintain soil structure, and also aid in loosening compaction by wind rocking in inclement weather.

The creation of new paths is a major headache for managers of urban woodlands, and many paths will only be visible when vegetation cover is at a minimum, or when

established sub-communities dominated by vulnerable species are present in virtually continuous stands. Efforts must be made to block off new trails that are visible at these times. In certain circumstances, it can even be advocated that neglected, overgrown trails be cleared initially by cutting and then maintained by infrequent, low levels of trampling. This will not only improve their potential to withstand wear, but will also benefit biodiversity.

Clearing overhanging and low growing vegetation over hydromorphic soils enables trails to dry out, but there are associated problems which may degrade valuable habitat. Selective thinning of the tree canopy will allow underlying ground vegetation the chance to adapt to the new light regime, but may favour rapid growing grassland species that are tolerant of trampling. The selective revegetation of areas will provide an organic matter source. Dead above-ground tissue and root biomass integrated into soil as organic matter will contribute to aggregate stability because of strong colloidal bonding in clayey soils (Hodges & Arden-Clarke 1986). Indeed, the annual addition of organic matter is important in maintaining good physical and chemical conditions in soil (Lutz 1945). Accordingly, land managers should be encouraged not to remove litter by raking, or to fell canopy dominants located nearby to trails. Inputs of litter will facilitate the natural consolidation of soil structure, promote the regeneration of new organic horizons and provide some degree of protection by cushioning any further trampling impacts. Clear-felling has definite ^{impacts on} ~~benefits for~~ biodiversity, but will reduce litter inputs and accelerate erosion as trails dry out.

Where the clay component of trail soils is high, sun-baked path crust surfaces increase the resistance to wear. Providing a camber or crossfall at the path surface so that run-off seeps away in side drains will improve drainage (Agate 1983). Drainage precautions can also be made with the advent of simple stone or wooden culverts or duckboarding (Bayfield & Lloyd 1973), and if drainage is too extensive then the provision of sluices in ditches will aid in retaining water (Warwick District Council 1992). However, draining soils of water may well cause irreversible damage to habitats. For example, Tilehill Wood represents a ^{truer} ~~better~~ example of semi-natural

mixed woodland when drainage is confined to occasional ditching projects in localised areas to alleviate excessively wet areas (Beard 1983⁴), and not adopted *en masse* in the wood.

Access for recreational use should be limited at times of peak precipitation such as in winter, when soils are at their wettest and most prone to damage. This follows the same rationale as not cultivating agricultural land when soils are wet, but waiting until drier autumn periods (Beard 1984, Rowell 1994). Careful management priorities avoiding damage to tree roots and felling must be instigated, because the deep and extensive root systems of large standards draw up immense amounts of water from surface and sub-surface soils (Agate 1983). ~~Where surface ponding does occur, the addition of building materials such as bricks and rubble will help to stabilise path surfaces.~~

In addition to trail management, the results of this study have consequences for path creation. Paths should be introduced to areas with resilient, well drained substrata where extensive erosion and drainage problems are unlikely to occur. Problems associated with undulating topography are only found locally in the study sites, e.g.: badly eroded embankment slopes in Crackley Wood. Nevertheless, trails can be positioned so that traffic moves uphill on steep slopes and downhill on gentle slopes to limit erosion (Bayfield & Aitken 1992).

Fencing, signs, boardwalks, natural barriers, silvicultural methods and locally operated social controls are management tools that can be used to restrict access to vulnerable woodland stands. For instance, Bayfield & Bathe (1982) found the most effective ways of stopping visitors moving along closed trails were by the use of a conspicuous notice that deterred 90 % of people, by brushwood that diverted 72 % of visitors, and logs that deterred 45 % of visitors. Another method to protect vulnerable stands in woodlands is by screening, where outer rows of trees are left unbrashed and unthinned. Often, the ultimate solution to inhibit stand penetration and wildlife disturbance is physical exclusion by fencing or silvicultural methods. The use of *Rubus fruticosus* agg. as a natural restrictive barrier is highlighted by this study, and

is recommended to inhibit the dispersal of walkers. The discrete use of poles and logs will stop the use of prohibited vehicles along rides (Irving 1985), and fallen branches and dead wood provide a convenient free source of raw materials to enable this to occur.

New paths can be constructed or old ones repaired using a variety of techniques that include aggregate paths, soil cement paths, stone pitching and slab paths, boardwalks and machine built paths (Bayfield & Aitken 1992). These methods provide a useful, but occasionally visually intrusive way of increasing carrying capacity in order to minimise damage to soils. Path surfacing with woodchip and bark produced on site is recommended because infiltration rates are increased and erosion is limited (Legg & Schneider 1977). However, most multi-use activities will not be sustained without track hardening, and the maintenance of path surfaces is especially vital in limiting the spread of visitors on slopes or in wet areas.

If there is a high contrast between the path and adjacent land, visitors will generally keep to the path. Distribution can be controlled by the strategic placement of boulders and logs, the provision of steps or a zigzagging, gradual ascent on slopes, the planting of screens, coarse tussock vegetation and diversionary planting, the erection of barriers, fences, waymarkers and signposts and the digging of skirting ditches and hollows (Agate 1983, Bayfield & Aitken 1992, Goldsmith 1974). Soil erosion protection can be instigated by the use of geotextiles, vegetation reinstatement and surface moulding and glues (Bayfield & Aitken 1992). Soil reinforcement in areas prone to heavy use can be achieved by subsurface geotextiles, mesh elements, soil cements and grassed gravel (Bayfield & Aitken 1992). However, land managers must be aware that the restoration of the original surface is seldom practicable, and unsuitable artificial surfaces may harm rural landscapes as much as the deleterious impact of soil erosion.

A further problem restricted to urban woodlands is that of the anti-social activity of vandalism and rubbish tipping. The prevention of physical damage to fences, boardwalks, gates and stiles must be undertaken to avoid destruction of habitat,

financial losses through broken materials and a reduction in the aesthetic quality of the site. The affects of vandalism were observed at irregular intervals over the survey period, e.g.: broken boardwalks in Tocil Wood and snapped barrier fencing in Tilehill Wood. Unfortunately, there are no easy ways to deal with these problems when they arise. Wooden boardwalks could be made out of hardy, thick half sectioned logs to increase longevity, but these are expensive. Perhaps emphasis should be placed on non-intrusive management techniques. To avoid anti-social behaviour in recreation sites, Goldsmith (1983a) advocates the minimal use of signposts and fencing, the use of local materials, public education and consultation with the use of volunteers.

8.4 Management of soil and litter organisms for recreation

Many woodland invertebrates whose larvae develop in soil, leaf litter and dead wood are species of woodland edges and glades, and by feeding on nectar the adults must have available food plants upon emergence (Kirby 1992). Most butterfly species depend solely on open areas such as woodland rides and glades to complete their life cycles, and other woodland specialist species only breed in newly created clearings (Warren & Fuller 1990, Warren & Key 1991). If the ground flora has been completely eradicated by excessive trampling, then dependent invertebrates will also disappear. Thus, it is acceptable to manage even minor trails to benefit invertebrates. For example, trails can be cleared and cut to broaden narrow or neglected routes, and peripheral trees and shrubs coppiced and side margins scalloped.

The value of recreational sites for invertebrates can extend to the micro-habitats that directly arise from continual visitor use and which mimic natural features. Although the intensive use of rides and footpaths churns up soil and is damaging to invertebrates, certain species can utilise seemingly undesirable features such as hoof prints and worn tyre ruts. Indeed, the temporary and permanent pools of wet areas that collect in hollows and ruts along tracks provide habitat for a characteristic aquatic fauna. The occasional passage of machinery along neglected rides, or horses along old livestock tracks, will maintain these features (Kirby 1992). Habitat that is commonly

found adjacent to woodland rides and footpaths also has considerable value for wildlife, so needs to be managed accordingly. Such areas might include sunny banks on sloping paths, skirting drainage ditches and dead wood (Kirby 1992, Thomas 1991). Invertebrates frequently observed in open woodland glades, rides, vehicle tracks and footpaths use the habitat for hunting, burrowing and resting. Even the bare ground in the centre of trails is used for basking by flying insects, and if not too disturbed, also by nesting solitary bees and wasps (Kirby 1992). Leaf litter, thinnings, loppings and felled trees will act as habitat piles and encourage colonisation into disturbed areas by fauna inhabiting peripheral areas. As the richest invertebrate fauna is found in partial or full shade, fine material and large piles of brash that are present on path and ride edges support an active litter pile. On no occasion should litter be removed from sites, except as a precaution against fire hazards.

8.5 Recovery of ecosystems

8.5.1 Regeneration of vegetation

A complete recovery of woodland vegetation cover from one season of heavy trampling varies from approximately two years in *Pteridium aquilinum* and *Rubus fruticosus* agg. dominated sub-communities, to over 5 years in *Hyacinthoides non-scripta* sub-communities. However, the recovery of reproductive ability of *Hyacinthoides non-scripta* will take far longer. The glasshouse experiments hint that the rate of plant recovery from light levels of trampling in open microclimates occurs approximately four weeks after trampling, providing that there is a *complete* cessation of impact. The fact that other species including *Hedera helix*, *Ranunculus ficaria*, *Geum urbanum* and *Silene dioica* crop up every year in trampled areas of the field survey also suggests that recovery is fairly rapid in partially shaded microclimates. These species survive by virtue of regenerative underground stems and roots, and regrowth from intercalary and apical meristems. However, irrespective of trampling, the colonisation of the shady field layers by *any* species will be limited, e.g.: *Dryopteris*

felix-mas was the only species capable of re-colonising a woodland floor under mature coppice (Ford & Newbould 1977).

Thus short-term ecosystem function, as categorised by increases in vegetation cover (and thus biomass accumulation), appears to recover from minor levels of disturbance with little requirement for human intervention. Recovery rates vary greatly in previous studies of temperate forest ecosystems, ranging from a full recovery after one winter (Cole 1987) to over 5 years (Kuss & Hall 1991) to the complete recovery of soil and understorey vegetation between 10 and 20 years (Cole & Marrion 1988, Kuss & Hall 1991, Leonard *et al.* 1985, Parikesit *et al.* 1995). Extremely disturbed areas will take even longer to recover. For example, the successional sequence of plants to recolonise abandoned roads could take up to 50 years to return to the original state (Shantz 1917 in Liddle 1975a).

Regardless of the nature of trampling impacts, the process of restoration to native diversity is undoubtedly very slow, and even though vegetative productivity will return in a few years, the restoration of original floristic conditions will take much longer. In addition, the greater the number of seasons¹ trampling the vegetation receives, then the longer the period of recovery required for a return to pre-trampling conditions.

8.5.2 Restoration of soils and trails

Undisturbed soils are at equilibrium with the environment and can take up to 12,000 years to develop, so the natural recovery rates of soil consolidation are assumed to be critically slow (De Gouvenain 1996, Rowell 1994, Speight 1973). Initiation of a complete phase of recovery after a cessation of impact ranges from 9 years (Thorud & Frissell 1976) to 15 years (Cole 1988) in forest ecosystems, and to up to a staggering 100 years in a montane ecosystem! (Willard & Marr 1971) This work suggests that partial trail recovery will occur after a minimum of six years after one season of 500 passes. The process of woodland soil restoration is far slower than that outlined for soil degradation, with an initial rapid rate of recovery followed by a prolonged slow

interim period. However, soils do appear to recover quickly from minor levels of trampling.

The period between peak summer use and minimal winter use is critical in allowing soil physical structure to regenerate. The impact of recreational trampling is mainly concentrated in the upper 10 cm of soil, with a minimal affect on subsoil horizons. If use is intensive and continuous all year round, then the seasonal recovery patterns described in this study will be greatly limited. Surface compaction is probably far easier to remedy than subsurface compaction, which may lead to more permanent damage. Suitable soil management can reverse damage, but completely stopping the use of existing routes is very difficult (Bayfield & Aitken 1992).

8.5.3 Recovery of soil fauna populations

The ability of the soil fauna to recover will be related to the type of substrate, and systems will be affected for many years unless remedying management proposals are instigated. Recovery of populations is likely to^{be} rapid in woodlands, and is closely related to the physical recuperation of soils. As long as there is a substantial 'fauna bank' to promote above and below ground colonisation by horizontal migration, the common and generalist taxa such as Acari and Collembola can successfully colonise impacted areas, and disperse efficiently by producing several generations per season. However, most soil organisms will only enter the regenerative succession when conditions become optimal for them. In contrast, Meyer (1993) showed that succession in alpine mor soils at high altitudes is very slow, and the full recovery of a bog moss Oribatid mite community after heavy trampling is estimated to take 10 years (Borcard & Whalley 1995).

Natural soil rejuvenation is aided by the biological activity of soil organisms (Thorud & Frissell 1976). Soil fauna activity may indirectly increase aeration and drainage by breaking down in-situ decaying roots and leaving manured channels in the soil (Gilyarov 1947, Rogers 1939). This will repair soil structure and create new pores in compacted soils. Some species such as *Allobophora longa* (Lumbricidae) are resistant

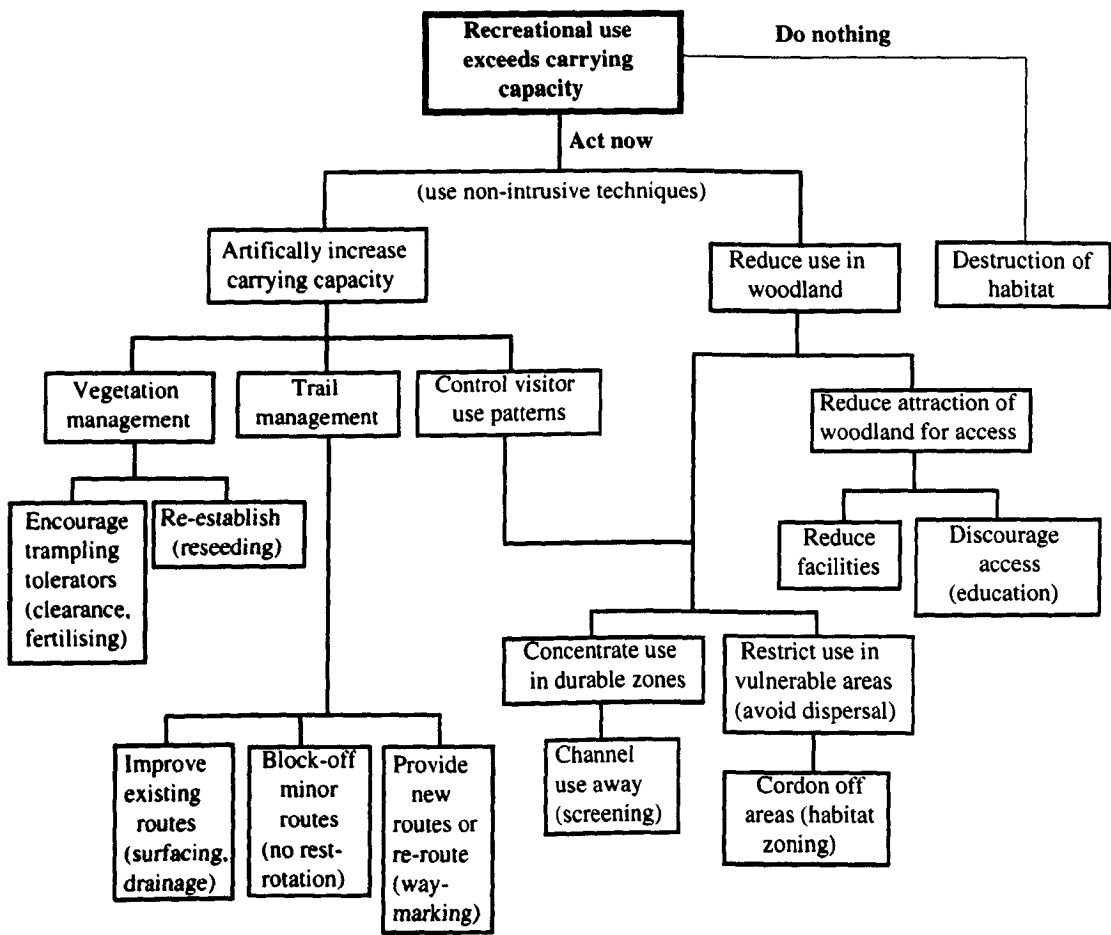
to trampling and have the potential to be used to repair the effects of soil compaction (Pearce 1984).

8.6 Checklist of management criteria

It is possible to generate a number of key strategies directly applicable to recreational management in W10 *Quercus robur* - *Pteridium aquilinum* - *Rubus fruticosus* woodland. These criteria answer Cole's (1983) question of how land managers can manipulate ecological characteristics in order to mitigate impacts, and they address Bayfield & Aitken's (1992) concern that the practical relevance to management techniques are rather limited. Proposals are broadly applicable to other woodland communities on similar soil types. A summary model is presented in Fig. 8.1 for use by land managers to resolve management the constraints which arise when the carrying capacity of woodland sites are compromised by recreational use. Management criteria are as follows:

- As trampling impacts on vegetation and soils occur most rapidly at low levels of use, there is only a limited potential to manage the temporal distribution of visitors by opening or closing areas. Rest-rotation techniques are not recommended to allow either recovery of vegetation or regeneration of soils, so the approach for management must be one of 'all or nothing'.
- As extremely low levels of use quickly eradicate the ecological value of a site, dispersed formal recreational activities should be stopped and visitor use concentrated along well-defined routes. Carefully positioned waymarked routes that take in features of interest such as glades, ponds and large trees are recommended.
- Use can be controlled by restricting access and by channelling impacts away from vulnerable to durable areas. The lateral spread of people into woodland stands can be prevented by screening with *Rubus fruticosus* agg. or large pieces of dead wood, which have conservation value and form a recreational buffer zone. Being visually non-intrusive, they will not suffer from vandalism in urban woodlands Fig. 8.1 - Decision making model of management strategies to resolve conflicts of

recreation with conservation in woodlands (tactics for influencing carrying capacity given in parentheses).



compared to artificial screening methods using brash or fencing. Simply widening rides and paths may also limit lateral spread.

- The use of ecological strategies of vegetation and the 'Index of Vulnerability' (Table 8.1) allows an immediate appraisal of the potential of any woodland site to withstand recreation, and helps to demarcate compartments for habitat zoning. As the carrying capacity of shaded woodland vegetation is lower than well lit cenoses, stands beneath conifers, senile coppice and dense shrub layers are particularly vulnerable.
- Restrict or prevent access for recreation, agriculture or forestry along trails during the wet winter months. Overuse degrades trails because the increasing soil

wetness reduces soil strength, and use at this time inhibits the recovery of soil and soil fauna regeneration by natural processes.

- Clearing or thinning of overhanging vegetation adjacent to very wet heavily textured soils along trail corridors will enable trails to dry out. Providing soil types are suitable, the formation of an impermeable surface cap will increase resistance to wear, and the increase in sunlight will also promote the growth of vegetation. However, proceed with caution when draining soils of surplus water in sensitive habitats as the action may indirectly degrade the ecological richness of the site.

- Strategic planting of selected canopy species and the sowing of suitable trampling resistant ground vegetation will bind eroded soil and provide a natural drainage sink. The felling of large standards near trails should be avoided unless there is a safety risk. These strategies are important when enforcing the temporary closure of trails because extensive litter input and wind rock by vegetation will aid in ecosystem restoration.

- Provide well surfaced, clearly marked trails that are easy to follow to prevent erosion. Block indistinct minor paths that criss-cross sites and which often split into smaller paths or gradually peter out. Management criteria for trails need to be instigated at the earliest possible time because the worse the condition of a trail, then the more difficult it will be to restore. Indeed, this study suggests that undisturbed organic and humic horizons in woodlands have a low load bearing carrying capacity, and should not be exposed to trampling at all.

- Special considerations will have to be made with respect to urban woodlands which are very heavily used often for anti-social activities, and where vandalism is an acute problem. Methods for controlling visitor distribution and numbers should be as non-intrusive as possible and any active management utilising artificial materials should be undertaken with caution.

- Because the process of soil and vegetation regeneration is critically slower than the rates of impact, emphasis should be placed on *planning to prevent damage*. Suitable management proposals are frequently lacking or are applied too late (Burden

& Randerson 1972), and even when work is carried out, maintenance is often inadequate. Thus, it is within the interests of the land managers to plan for the control and monitoring of recreational activities in vulnerable areas, bearing in mind that the level of use and level of demand are not the same thing (Goldsmith 1983b).

- Educating the general public is a major priority, but policies are often difficult or impossible to enforce in urban areas, especially as a result of public apathy or local resentment. Endorsing public education to increase awareness can be attempted by using interpretative boards, nature trail leaflets, open days, temporary information boards, nature reserve signs and press coverage. Press coverage generated during the course of this work has probably helped (Appendix 8.1).
- Any management proposal for ecosystem rehabilitation, creation or maintenance will have to be multi-disciplinarian in approach. Management criteria should be synthesised with respect to managing users, managing the resource or managing both users *and* the resource (Goldsmith 1974).

8.7 Conclusion

This study shows that even low levels of use are likely to be sufficient to cause an adverse impact on woodland ecosystems. Moreover, trampling can degrade biota and keep routes open at very low levels of intensity. If woodland trails are attractive, easy to follow and preferably waymarked, have adequate drainage and are comfortably surfaced with non-intrusive materials then people will generally stick to them. The provision and suitable management of such woodland trails will provide a range of opportunities for people to enjoy open air recreation without threatening the wildlife value of the wood.

The future for many of Britain's best woodlands hangs in the balance. In the year 2000, the Forestry Commission reports to the Government on the extent to which there is access to forest and woodland (DETR consultation paper 1998). The Government may consider extending access to woodland areas after the Forestry Commission have reported their findings, and invoke a new statutory right of access

to be granted to previously inaccessible sites. Unless suitably managed, the increase in public access to previously undisturbed woodlands, especially on the urban fringe, will quickly destroy the ecological characteristics of sites. If legislation does extend to woodlands, the nature conservation and heritage agencies must not be afraid of exercising proposal 13 of the DETR consultation paper (1998), which decrees: *'English Nature, The Countryside Council for Wales, English Heritage and Cadw should have powers to limit access to particularly sensitive sites either permanently or temporarily'*.

Although woodlands can absorb large amounts of people without seeming crowded, the trick lies in not allowing recreational use and public access to compromise the special qualities that attract visitors to the wood in the first place. Yet unless preventative action is taken by implementing recreation management strategies for conservation, then the deterioration and destruction of all wooded habitats in the British countryside will continue indefinitely.

References

- ~~Abdelmagid, A.H., Trlica, M.J. & Hart, R.H. (1987) Soil and vegetation responses to simulated trampling. *Journal of Range Management*, **40**, 303-6.~~
- Adkinson, G.P. & Jackson, M.T. (1996) Changes in ground layer vegetation near trails in mid-western US forests. *Natural Areas Journal*, **16**, 14-23.
- Agate, E. (1983) *Footpaths - a Practical Handbook*. BTCV.
- Alexander, M. (1961) *Soil Microbiology*. Wiley, New York.
- Amato, M. & Ladd, S.N. (1988) Assay for microbial biomass based on ninhydrin-reactive nitrogen in extracts of fumigated soils. *Soil Biology and Biochemistry*, **20**, 107-14.
- Andersen, U.V. (1995) Resistance of Danish coastal vegetation types to human trampling. *Biological Conservation*, **71**, 223-30.
- Anderson, F. (1997) *Tree News*, (spring edition).
- Anderson, P. & Radford, E. (1992) *A review of the effects of recreation on woodland soils, vegetation and fauna*. English Nature Research Report No. 27.
- Andre, H.M., Noti, M.I. & Lebrun, P. (1994) The soil fauna - the other biotic frontier. *Biodiversity and Conservation*, **3**, (1), 45-56.
- Aspinall, R.J. & Pye, A.M. (1987) The effect of trampling on limestone grassland in the Malham area of North Yorkshire. *Journal of Biogeography*, **14**, 105-15.
- Avery, B.W. (1990) *Soil of the British Isles*. C.A.B International, Oxon.
- Ball, D.F. (1986) Site and Soils, in *Methods in Plant Ecology* (ed S.B. Chapman), Oxford: Blackwell.
- Barker, G. (1967) Hampshire public open spaces and wildlife conservation, in *The Biotic Effects of Public Pressures on the Environment* (ed E. Duffey), 169-72. ~~Abbots Ripton, NC.~~
- Bates, G.H. (1935) The vegetation of footpaths, sidewalks, cart-tracks and gateways. *Journal of Ecology*, **23**, 470-487.
- Bayfield, N.G. (1971a) A simple method for detecting variations in walker pressure laterally across paths. *Journal of Applied Ecology*, **8**, 533-35.

- Bayfield, N.G. (1971b) Some effects of walking and skiing on vegetation at Cairngorm, in *The Scientific Management of Animal and Plant Communities for Conservation* (eds E. Duffey and A.S. Watt), *11th Symposium of the British Ecological Society*, 469-85. Oxford, Blackwell.
- Bayfield, N.G. (1979a) Recovery of four montane heath communities on Cairngorm, Scotland, from disturbance by trampling. *Biological Conservation*, **15**, 165-79.
- Bayfield, N.G. (1979b) Some effects of trampling on *Molophilus Ater* (Meigen) (Diptera, Tipulidae). *Biological Conservation*, **15**, 219-32.
- Bayfield, N.G. (1983) Effects of extended use on footpaths in mountain areas of Britain, in R.E.R.G. Report No. 9 (eds N.G.Bayfield & G.C.Barrow), 100-11.
- Bayfield, N.G. & Pickrell, B.G. (1971) The construction and use of a photoflux people counter. *Recreation News Supplement*, (5), 9-12.
- Bayfield, N.G. & Lloyd, R.J. (1973) *The Pennine Way Survey*. Countryside Commission.
- Bayfield, N.G. & Barrow, G.C. (1976) The use and attraction of nature trails in upland Britain. *Biological Conservation*, **9**, 267-292.
- Bayfield, N.G., Urquhart, U.H. & Cooper, S.M. (1981) Susceptibility of four species of *Cladonia* to disturbance by trampling in the Cairngorm Mountains, Scotland. *Journal of Applied Ecology*, **18**, 303-10.
- Bayfield, N.G. & Bathe, G. M. (1982) Experimental closure of footpaths in a woodland National Nature Reserve in Scotland. *Biological Conservation*, **22**, 229-37.
- Bayfield, N.G., Urquhart, U. & Rothery, P. (1984) Colonization of bulldozed track verges in the Cairngorm Mountains, Scotland. *Journal of Applied Ecology*, **21**, 343-354.
- Bayfield, N.G. & Aitken, R. (1992) *Managing the Impacts of Recreation on Vegetation and Soils: A Review of Techniques*. ITE Project T0 2050V1, NERC.
- Beard, G.R. (1979) The soils of Tilehill Wood nature reserve. *Proceedings Coventry Natural History and Scientific Society*, **5**, (3), 98-104.

- Beard, G.R. (1984) Soils in Warwickshire. V. Sheets SP 27 & 37 (Coventry South), Soil Survey Record No. 81, Harpenden.
- Beardsley, W.G. & Wagar, J.A. (1971) Vegetation management on a forested recreation site. *Journal of Forestry*, **69**, 728-31.
- Beddows, A.R. (1958) Biological flora of the British Isles - *Holcus lanatus*. *Journal of Ecology*, 421-30.
- Begon, M., Harper, J.L. & Townsend, C.R. (1990) *Ecology: Individuals, Populations and Communities* (2nd ed). Blackwell Scientific Publications. Oxford.
- Bell, K.L. & Bliss, L.C. (1973) Alpine disturbance studies: Olympic National Park, USA. *Biological Conservation*, **5**, 25-32.
- Bengtsson, J., Persson, T. & Lundkvist, H. (1997) Long-term effects of logging residue addition and removal on macroarthropods and enchytraeids. *Journal of Applied Ecology*, **34**, (4), 1014-22.
- Biggin, P. (1982) Forestry and bracken. *Proc. of the Roy. Soc. of Edin.*, **81B**, 19-28.
- Blackman, G.E. & Rutter, A.J. (1950) Physiological and ecological studies in the analysis of plant environment. V. An assessment of the factors controlling the distribution of the bluebell (*Scilla non-scripta*) in different communities. *Annals of Botany*, **14**, 487-520.
- Blackman, G.E. & Rutter, A.J. (1954) Biological flora of the British Isles - *Endymion non-scriptus*. *Journal of Ecology*, **42**, 629-38.
- Blom, C.W.P.M (1979) *Effects of trampling and soil compaction on the occurrence of some Plantago species in coastal sand dunes*. Ph.D. Thesis, University of Nijmegen, The Netherlands.
- Borcard, D. & ^{Whalley}~~Matthay~~, W. (1995) Effect of controlled trampling of Sphagnum mosses on their Oribatid mite assemblages. *Pedobiologia*, **39**, (3), 219-30.
- Bratton, S.P. (1985) Effects of disturbance by visitors on two woodland orchid species in Great Smoky Mountains National Park, USA. *Environmental Management*, **3**, 431-45.

- Bratton, S.P., Stromberg, L. & Harmon, M.E. (1982) Firewood-gathering impacts in backcountry campsites in Great Smoky Mountains National Park. *Journal of Environmental Management*, **6**, 63-71.
- Bright, J.A. (1986) Hiker impact on herbaceous vegetation along trails in an evergreen woodland of Central Texas. *Biological Conservation*, **36**, 53-69.
- British Standards Institution (1967) *Methods of Testing Soils for Engineering Purposes*. British Standard 1377, London.
- Bryan, R.B. (1977) The influence of soil properties of degradation of mountain hiking trails at Grovelsjon. *Geografiska Annaler*, **59**, 49-65.
- Burden, R. (1970) Some effects of people on the nature trail at Ranmore, Surrey. *Surrey Naturalist*, 1969. *Annual Report*, 14-22.
- Burden, R.F. & Randerson, P.F. (1972) Quantitative studies of the effects of human trampling on vegetation as an aid to the management of semi-natural areas. *Journal of Applied Ecology*, **9**, 439-57.
- Burger, H. (1932) Physikalische Eigenschaften von Wald und Freilandboden. IV. Mitteilung, Ferienlager und Walboden. *Mitteilung der Schweizerischen Central Anstalt fur das Forstliche Versuchswesen*, **17**, 299-322.
- Burton, R.C.J. (1974) The recreational carrying capacity of the countryside. Occasional Publication No. 11, Keele University.
- ~~Canaway, P.M. (1976) Fundamental techniques in the study of turf grass wear: an advance report on research. *Journal of Sports Turf Research Inst.*, **51**, 104-15.~~
- ~~Cannell, M.G.R., Malcolm, D.C. & Robertson, P.A. (1992) *The Ecology of Mixed Species Stands of Trees*. Special publication No. 11 BES, Blackwell.~~
- Chadee, D.R.M. (1988) *The impact and management of access areas of protected and recreation landscapes in Britain, with particular reference to vegetation*. M.Phil. Thesis, Wye College, University of London.
- Chapman, S.B. (1986) *Methods in Plant Ecology*. Oxford: Blackwell.
- Chappell, H.G., Ainsworth, J.F., Cameron, R.A.D. & Redfern, M. (1971) The effect of trampling on a chalk grassland ecosystem. *Journal of Applied Ecology*, **8**, 869-82.

- Charman, D.J. & Pollard, A.J. (1994) Long term vegetation recovery after vehicle track abandonment on Dartmoor, SW England. *British Ecological Society Bulletin*, **25**, 22-8.
- Clapham, A.R., Tutin, T.G. & Warburg, E.F. (1962) *Flora of the British Isles* (2nd edn). Cambridge University Press, London.
- Coker, A.M. & Coker, P.D. (1972) Use of pressure sensitive counters. *Recreation News Supplement*, (7), 14-7.
- Cole, D.N. (1978) Estimating the susceptibility of wildland vegetation to trailside alteration. *Journal of Applied Ecology*, **15**, 281-86.
- Cole, D.N. (1979) Reducing the impact of hikers on vegetation: an application of analytical research methods, in *Conference Proceedings - Recreational Impacts on Wildlands* (eds R. Ittner *et al.*), US Dept. of Agriculture, Forest Service, Pacific NW Region, 71-78.
- Cole, D.N. (1982) *Wilderness campsite impacts: effects of amount of use*. USDA Forest Service, Intermountain Forest and Range Experiment Station Research Paper INT-284, Missoula, Montana.
- Cole, D.N. (1983) Management of ecological impacts in wilderness areas in the United States, in R.E.R.G. Report No. 9 (eds N.G.Bayfield & G.C.Barrow), 138-54.
- Cole, D.N. (1985) *Recreational trampling effects on six habitat types in Western Montana*. USDA Forest Service Intermountain Research Station Paper 1985 No. 350, 1-43.
- Cole, D.N. (1987) Effects of three seasons of experimental trampling on five montane forest communities and a grassland in Western Montana, USA. *Biological Conservation*, **40**, 219-244.
- Cole, D.N. (1988) *Disturbance and recovery of trampled montane grassland and forests in Montana*. Intermountain Research Station Research Paper INT-389, 1-37.
- Cole, D.N. (1993) *Trampling effects on mountain vegetation in Washington, Colorado, New Hampshire and North Carolina*. US Dept of Agriculture, Forest Service, Intermountain Research Station, Research Paper 1 NT-464, Ogden, Utah.

- Cole, D.N. (1995a) Experimental trampling of vegetation. I. Relationship between trampling intensity and vegetation response. *Journal of Applied Ecology*, **32**, 203-14.
- Cole, D.N. (1995b) Experimental trampling of vegetation. II. Predictors of resistance and resilience. *Journal of Applied Ecology*, **32**, 215-24.
- Cole, D.N. (1995c) *Recreational trampling experiments: effects of trampler weight and shoe type*. USDA Forest Service Research Note INT-RN-425, Ogden, Utah.
- Cole, D.N. (1995d) Disturbance of natural vegetation by camping: experimental applications of low-level stress. *Environmental Management*, **19**, (3), 405-16.
- Cole, D.N. & Fichtler, R.K. (1983) Campsite impact on three western wilderness areas. *Environmental Management*, **7**, 275-88.
- Cole, D.N. & Marion, J.L. (1988) Recreation impacts in some riparian forests of the eastern United States. *Environmental Management*, **12**, 99-102.
- Cole, D.N. & Trull, S.J. (1992) Quantifying vegetation response to recreational disturbance in the North Cascade Mountains, Washington. *NW Science*, **66**, 229-36.
- Cole, D.N. & Bayfield, N.G. (1993) Recreational trampling of vegetation: standard experimental procedures. *Biological Conservation*, **63**, 209-15.
- Cooper-Driver, G. (1976) Chemotaxonomy and phytochemical ecology of bracken. *Botanical J. of the Lin. Soc.*, **73**, 35-46.
- ~~Countryside Commission (1976) *Footpaths for Recreation*, Report CCP99.~~
- ~~Crawford, A.K. & Liddle, M.J. (1977) The effect of trampling on neutral grassland. *Biological Conservation*, **12**, 135-42.~~
- Dale, D. & Weaver, T. (1974) Trampling effects on vegetation of the trail corridors of North Rocky Mountains forests. *Journal of Applied Ecology*, **11**, 767-72.
- Davies, W. (1938) Vegetation of grass verges and other excessively trodden habitats. *Journal of Ecology*, **26**, 38-49.
- De Govenain, R.C. (1996) Indirect impacts of soil trampling on tree growth and plant succession in the North Cascade Mountains of Washington. *Biological Conservation*, **75**, 279-87.

- Del Moral, R. (1979) Predicting human impact on high elevation ecosystems. Conference proceedings, *Recreational impact on wildlands*. USDA Forest Service, Pacific NW Region, Seattle, Washington.
- DETR Consultation Paper (1998) *Access to the Open Countryside in England and Wales*. Department of the Environment, Transport and the Regions.
- Dokukina, E.A. & Menahxonum, N.H. (1992) Effects of recreation on fungal diseases. *Ekologiya*, Part 2, 75-76.
- Dotzchenko, A.D., Papamichos, N.T. & Romine, D.S. (1967) Effects of recreational use on soil and moisture conditions in Rocky Mountain National Park. *Journal of Soil and Water Conservation*, **22**, 196-7.
- Douglas, E.A. (1989) *An assessment of the impact of the November Classic Badge Event 1988 on the New Forest*. An independent report produced for the British Ecological Society, The Sports Council, The British Orienteering Federation and Southampton Orienteering Club.
- ~~Douglas, G.W., Nagy, I.A.S. & Scotter, G.W. (1975) Effects of human and horse trampling on natural vegetation. Waterloo Lakes National Park. Canadian Wildlife Service Report, Alberta.~~
- Duffey, E. (1974) *Nature Reserves and Wildlife*. Heinemann, London.
- Duffey, E. (1975) The effects of human trampling on the fauna of grassland litter. *Biological Conservation*, **7**, 255-74.
- Duggeli, M. (1937) Wie wirkt das oftete Betreten des Walbodens auf einzelene physikalische und biologische Eigenschaften. *Schweizerische Zeitschrift fur Forstwesen*, **88**, 151-65.
- Dunn, B.A. (1984) *Recreation effects on forest soil and vegetation: research synopsis and selected bibliography*. Technical paper, Dept. Forestry, Clemson Univ., USA.
- Dzwonko, Z. & Loster, S. (1997) Effects of dominant trees and anthropogenic disturbances on species richness and floristic composition of secondary communities in southern Poland. *Journal of Applied Ecology*, **34**, (4), 861-70.

- Emanuelsson, U. (1983) Recreation impact on mountainous areas in Northern Sweden, in R.E.R.G. Report No. 9 (eds N.G.Bayfield & G.C.Barrow), 63-73.
- Evans, G.C. (1972) *The Quantitative Analysis of Plant Growth*. University of California Press, Berkeley, CA.
- Falk, S. (1996) Phew! What a summer. *Warwickshire Wildlife Trust Magazine*, **91**
- Ferrero, A.F. (1991) Effects of compaction simulating cattle trampling on soil physical characteristics in woodlands. *Soil & Tillage Research*, **19**, 319-29.
- Ferris-Kaan, R. (Ed.) (1991) Recreational use of woodland and its ecological effects. Report of meeting of British Ecological Society: Forest Ecology Group. *BES Bulletin*, **22**, (4), 254-56.
- Fleming, R.L., Black, T.A. & Eldridge, N.R. (1993) Water content, bulk density and coarse fragment measurement in forest soils. *Soil. Sci. Soc. Amer. J.*, **57**, (1), 261-70.
- Flogaitis, E. & Blandin, P. (1985) L'impact du pietinement sur les macroarthropodes du sol dans les forets periurbaines: etude experimentale. *Acta Œcologica / Œcologia Applicata*, **6**, (2), 129-41.
- Foin, T.G., Garton, E.O., Bowen, C.W., Everingham, J.M., Schultz, R.O. & Holton, B. (1977) Quantitative studies of visitor impacts on environments of Yosemite National Park, California and their applications for park management. *Journal of Environmental Management*, **5**, 1-22.
- Ford, E.D. & Newbould, P.J. (1977) The biomass and production of ground vegetation and its relation to tree cover through a deciduous woodland cycle. *Journal of Ecology*, **65**, 201-12.
- Frenkel, R.E. (1970) Ruderal vegetation along some California roadsides. *University of California Publications in Geography*, **20**, 1-163.
- Frissell, S.S. & Duncan, D.P (1965) Camp-site preference and deterioration in the Quetico-Superior Canoe country. *Journal of Forestry*, **63**, 256-60.
- ~~Fushtey, S.G., Taylor, D.K. & Fairey, D. (1983) The effect of wear stress on survival of pure stands and on mixtures. *Can. J. of Pla. Sci.*, **63**, 317-22.~~

- Garay, I. & Nataf, L. (1982) Microarthropods as indicators of human trampling in suburban forests, in *Urban Ecology* (eds R. Bornkamm *et al.*), Blackwell, 201-207. ~~Oxford~~
- Gauch, H.G. (1982) *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge.
- Gilbertson, D.D., Kent, M. & Pyatt, F.B. (1985) *Practical Ecology for Geography and Biology: Survey, Mapping and Data Analysis*. Hutchinson.
- Gilyarov, M.S. (1947) Distribution of humus, root systems and soil invertebrates within the soil of the walnut forests of the Ferghana Mountain Range. *Dokl. Akad. Nauk USSR*, **55**, 49-52.
- Gleisman, S.R. (1976) Allelopathy in a broad spectrum of environments as illustrated by bracken. *Bot. J. of the Linn. Soc.*, **73**, 95-104.
- Goldsmith, F.B., Munton, R.J.C. & Warren, A. (1970) The impact of recreation on the ecology and amenity of semi-natural areas: methods of investigation in the Isles of Scilly. *Biological Journal of the Linnean Society*, **2**, 287-306.
- Goldsmith, F.B. (1974) Ecological effects of visitors in the countryside, in *Conservation in Practice*, (eds F.B. Goldsmith and F.B. Warren), Wiley, New York, 217-31.
- Goldsmith, F.B. (1983a) Ecological effects of visitors and the restoration of damaged areas, in *Conservation in Perspective* (eds A. Warren & F.B. Goldsmith). Wiley New York, 201-14.
- Goldsmith, F.B. (1983b) Future requirements for recreation ecology research, in *R.E.R.G Report No. 9*, 162-64.
- Goryshina, T.K. (1983) The effect of trampling caused by recreation on the internal structure of the leaf and thallus of some plants. *Ekologiya*, **2**, 11-18.
- Government Manifesto (1997) Labour Party.
- Grabham, P.W. & Packham, J.R. (1983) A comparative study of the bluebell *Hyacinthoides non-scripta* (L.) Chouard in two different woodland situations in the West Midlands, England. *Biological Conservation*, **26**, 105-26.

- Grabherr, G. (1982) The impact of trampling by tourists on a high altitudinal grassland in the Tyrolean Alps, Austria. *Vegetatio*, **48**, 209-19.
- Grabherr, G. (1983) Damage to vegetation by recreation in the Austrian and German Alps, in *The Ecological Impact of Outdoor Recreation on Mountain Areas in Europe and North America* (eds N.G. Bayfield and G.C. Barrow), Recreation Ecology Research Group Report No. 9, Wye College, England, 74-91.
- Grable, A.R. & Siemer, E.G. (1968) Effects of bulk density, aggregate size, and soil water suction on oxygen diffusion, redox potentials and elongation of corn roots. *Proc. Soil Sci. Soc. Am.*, **32**, 180-6.
- Green, B. (1992) *Countryside Conservation - The Protection and Management of Amenity Ecosystems*. (2nd Edition). Pub. E. & F.N. Spon.
- Grime, P.J. (1979) *Plant Strategies and Vegetation Processes*. Wiley, Chichester.
- Grime, P.J., Hodgson, J.G. & Hunt, R. (1988) *Comparative Plant Ecology*, Unwin Hyman, London.
- Hall, C.N. & Kuss, F.R. (1989) Vegetation alteration along trails in Shenandoah National Park, Virginia. *Biological Conservation*, **48**, 211-27.
- Hammit, W.E. & Cole, D.N. (1987) *Wildland Recreation: Ecology and Management*. Wiley, New York.
- Hargreaves, J., Bodley, A.M., Munter, J., Yellow, C.W & Haque, S.N. (1986) A new era of modern statistical thought. *Occasional Publication No. 69, Multi-Variate Statistical Research Group*, Geneva.
- Harrison, C. (1981) Recovery of lowland grassland and heathland in southern England from disturbance by seasonal trampling. *Biological Conservation*, **19**, 119-130.
- ~~Hartley, E. (1973) *Mans effects on the stability of alpine and subalpine vegetation in Glacier National Park, Montana*. Ph.D. Thesis, Duke University, N. Carolina.~~
- ~~Hatton, C. (1991) Wargames and wildlife: Jeux sans frontières. *ECOS*, **12**, (1), 26-30.~~

- Hearn, K. (1981) Management of western oakwoods for nature conservation and amenity, in *Research and Planning for Nature Conservation and Amenity in Woodlands*.
- Heisler, C. (1995) Collembola and Gamasina - bioindicators for soil compaction. *Acta Zoologica Fennica*, **196**, 229-31.
- Higgs, D.E.B. & James, D.B. (1969) Comparative studies into the biology of upland grasses. 1. Rate of dry-matter production and its control in four grass species. *Journal of Ecology*, **57**, 553-63.
- Hill, M.O. (1979) DECORANA - A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Cornell University, Ithaca, New York.
- Hill, M.O. & Gauch, H.G. (1980) Detrended correspondence analysis: an improved ordination technique. *Vegetatio*, **42**, 47-58.
- Hobbs, R.J. & Huenneke, L.F. (1992) Disurbance, diversity and invasion: Implications for conservation. *Conservation Biology*, **6**, 324-37.
- Hodges, R.D. & Arden-Clarke, C. (1986) *Soil erosion in Britain: Levels of soil damage and their relationship to farming practices*. The Soil Association, 1-36.
- Holmes, D.O. & Dobson, H.E.M. (1976) *Ecological Carrying Capacity Research: Yosemite National Park, Part I. The Effects of Human Trampling and Urine on Subalpine Vegetation, and Survey of Past and Present Backcountry Use*. Report to USDA National Park Service, California University, Berkeley.
- Hughes, P. (1943) The respiration of *Tyroglyphus farinae*. *J. Exp. Biol.*, **20**, 1-5.
- Ingellog, T., Olsson, M.T. & Bodvarsson, H. (1977) *Effects of long-term trampling and vehicle driving on soil, vegetation and certain soil animals of an old Scots pine stands*, Research Notes No. 27, Royal College of Forestry, Uppsala.
- Irving, J.A. (1985) *The Public in Your Woods*. Packard Publishing Ltd.
- Jackson, R.M. & Raw, F. (1973) *Life in the Soil*. Camelot Press.
- Jim, C.Y. (1987) Trampling impacts of recreationists on picnic sites in a Hong Kong national park. *Environmental Conservation*, **14**, No. 2, 117-27.

Joergensen, R.G. & Brookes, P.J. (1990) Ninhydrin reactive nitrogen measurements of microbial biomass in 0.5 M K₂SO₄ soil extracts. *Soil Biology and Biochemistry*, **22**, 1023-7.

~~Jones, D.H. (1978) *The effect of pedestrian impact on selected soils*. M.Sc. Thesis, University of Glasgow, Scotland.~~

Jongman, R.H.G., Ter Braak, C.J.F. & Van Tongeren, G.F.R. (1995) *Data Analysis in Community and Landscape Ecology*, Cambridge University Press.

Kardell, L. (1974) *Damage to the vegetation caused by orienteering*, Research Notes 4, Stockholm Royal College of Forestry, Stockholm.

Kellomaki, S. (1973) Ground cover response to trampling in a spruce stand of *Myrtilus* type. *Silva Fennica*, **7**, 96-113.

Kellomaki, S. & Saastomowen, U.L. (1975) Trampling tolerance of forest vegetation. *Acta Forestalia Fennica*, **147**, 5-29.

~~Kelly, J.R. & Harwell, M.A. (1990) Indicators of ecosystem recovery. *Environmental Management*, **14**, 527-45.~~

Kevan, D.K. (1962) A practical key to the orders and suborders of soil and litter inhabiting animals, in *Soil Zoology* (ed D.K. Kevan), New York.

Kirby, P. (1992) *Habitat Management for Invertebrates: a Practical Handbook*. RSPB.

Knight, G.H. (1964) Some factors affecting the distribution of *Endymion non-scriptus* in some Warwickshire Woods. *Journal of Ecology*, **52**, 405-21.

Kovach, W.L. (1995) *MVSP - A Multi-Variate Statistical Package for IBM-PC's*, Version 2.2. Kovach Computing Services, Wales.

Krynine, D.P. (1941) *Soil Mechanics*. New York.

Kuhnett, W. (1962) An introduction to the study of soil animals, in *Soil Zoology*, (ed D.K. Kevan).

Kuss, F.R. (1986) A review of the major factors influencing plant responses to recreation impacts. *Environment Management*, **10**, (5), 637-50.

- Kuss, F.R. & Hall, C.N. (1991) Ground flora trampling studies; five years after closure. *Environmental Management*, **15**, (5), 715-27.
- Lance, A.N., Baugh, I.D. & Love, J.A. (1989) Continued footpath widening in the Cairngorm Mountains, Scotland. *Biological Conservation*, **49**, 201-14.
- Landals, M. & Scotter, G.W. (1973) Visitor impacts on meadows near Lake O'Hara, Yoho National Park, Edmonton. Canadian Wildlife Service, 184 p.
- Landals, M. & Scotter, G.W. (1974) An ecological assessment of the summit area, Mount Revelstoke National Park, Edmonton. Canadian Wildlife Service, 197 p.
- LaPage (1962) Recreation and the forest site. *Journal of Forestry*, **60**, 319-21.
- LaPage (1967) *Some Observations in Campgrounds Trampling and Ground Cover Response*, USDA, Forest Service, Research Paper NE68, Syracuse, New York.
- Legg, M.H. & Schneider, G. (1977) Soil deterioration on campsites: northern forest types. *Soil Sci. Soc. Am. J.*, **41**, 437-41.
- Leney, F.M. (1974) *The ecological impacts of public pressure on picnic sites*. Ph.D. Thesis, University of Aberdeen.
- Leonard, R.E., McMahon, J.L. & Kehoe, K.M. (1985) *Hiker trampling impacts on Eastern forests*. USDA Forest Service NE Forest Experimental Station Research Paper 1985 No. 555, 1-5.
- Liddle, M.J. (1973) *The Effects of Trampling and Vehicles on Natural Vegetation*. Ph.D. thesis. University of Bangor.
- Liddle, M.J. (1975a) A selective review of the ecological effects of human trampling on natural ecosystems. *Biological Conservation*, **7**, 17-36.
- Liddle, M.J. (1975b) A theoretical relationship between the primary productivity of vegetation and its ability to tolerate trampling. *Biological Conservation*, **8**, 251-55.
- Liddle, M.J. (1984) Classification of the interactions between animals and plants with particular reference to human trampling, in *The Ecological Basis of Interactions between Organisms* (eds M. J. Liddle and J. C. Tothill), AES Monograph 1/84, School of Australian Environmental Sciences, Griffith University, Brisbane, 113-28.

- Liddle, M.J. (1991) Recreation Ecology: Effects of trampling on plants and corals. *Trends in Ecology and Evolution*, **6**, No. 1, 13-17.
- Liddle, M.J. (1997) *Recreation Ecology*. Chapman & Hall, London.
- Liddle, M.J. & Moore, K.G. (1974) The microclimate of sand dune tracks: the relative contribution of vegetation removal and soil compression. *Journal of Applied Ecology*, **11**, 1057-68.
- Liddle, M.J. & Greig-Smith, P.J. (1975a) A survey of tracks and paths in a sand dune ecosystem. I. Soils. *Journal of Applied Ecology*, **12**, 893-908.
- Liddle, M.J. & Greig-Smith, P.J. (1975b) A survey of tracks and paths in a sand dune ecosystem. II. Vegetation. *Journal of Applied Ecology*, **12**, 909-30.
- Liddle, M.J. & Chitty, L.D. (1985) The nutrient budget of horse tracks on an English lowland heath. *Journal of Applied Ecology*, **18**, 841-8.
- Liddle, M.J. & Thyer, N.C. (1986) Trampling and fire in a subtropical dry sclerophyll forest. *Environmental Conservation*, **13**, (1), 33-9.
- Liddle, M.J. & Kay, A.M. (1987) Resistance, survival and recovery of trampled corals on the Great Barrier Reef. *Biological Conservation*, **42**, 1-18.
- Lutz, H.J. (1945) Soil conditions of picnic grounds in public forests parks. *Journal of Forestry*, **43**, 121-7.
- MacFadyen, A. (1962) Soil arthropod sampling. *Advances in Ecological Research*, **1**, 1-34.
- Madden, K.E. & Fox, B.J. (1997) Arthropods as indicators of the effects of fluoride pollution on the succession following sand mining. *Journal of Applied Ecology*, **34**, (5), 1239-56.
- Magill, A.W. & Nord, E.C. (1963) *An evaluation of campground conditions and needs for research*. USDA Forest Service Research Note PSW4.
- Mahoney, C.L. (1976) Soils insects as indicators of use patterns in recreation areas. *Journal of Forestry*, **74**, (1), 35-37.

- Makhdoum, M.F. & Khorasani (1988) Differences between environmental impacts of logging and recreation in mature forest ecosystems. *Environmental Conservation*, **15**, (2), 137-42.
- Marion, J.L. & Merrion, L.C. (1985) *Recreational impacts on well-established campsites in the Boundary Waters Canoe Area Wilderness*. Stn. Bull. AD-SB-2502, University of Minnesota, Agricultural Experiment Station.
- McCreath, J.B. (1982) Some reflections and projections on bracken control. *Proc. of the Royal Soc. of Edin.*, **81B**, 135-43.
- Meinecke, P. (1928) *The effect of excessive tourist travel on the California Redwood Parks*. California Dept of Natural Resources, Division of Parks, Sacramento.
- Meyer, E. (1993) Beeinflussung der Fauna alpiner Boden durch Sommer- und Wintertourismus in West-Osterreich. *Revue Suisse de Zoologie*, **100**, (3), 519-27.
- Miller, J.W. & Miller, M.M. (1976) Revegetation in the subalpine zone. Washington State University Arboretum, **39**, 12-16.
- Mukerji, S.K. (1936) Contributions to the autecology of *Mercurialis perennis*. *Journal of Ecology*, **14**, 38-81.
- Murphy, P.W. (1953) The biology of forest soils with special reference to the mesofauna or meiofauna. *J. Soil Sci.*, **4**, 155-93.
- Murphy, P.W. (1962) Ecology of the fauna of forest soils, in *Soil Zoology* (ed D.K. Kevan), 99-124.
- Nagy, J.A.S. & Scotter, G.W. (1974) A quantitative assessment of the effects of human and horse trampling on natural areas. Waterton Lakes National Park, Edmonton. Canadian Wildlife Service, 145 p.
- Naito, T. (1969) Changes of alpine vegetation in Mt. Hakkado due to human treading. *Ecological Review*, **17**, 171-6.
- Neal, E. (1977) *Badgers*. Blandford Press, London.
- Noe, R. & Blom, C.W.P.M. (1981) Occurrence of three *Plantago* species in coastal sand dune grasslands in relation to pore volume and organic matter content of the soil. *Journal of Applied Ecology*, **19**, (1), 177-82.

~~O'Connor, K.F. (1957) Influences of treading on grassland. *Diss. Abstr.*, 17, 4-5.~~

Ocio, J.A. & Brookes, P.C. (1990) An evaluation of methods for measuring the microbial biomass in soils following recent additions of wheat straw and characterizations of the biomass that develops. *Soil Biology and Biochemistry*, **22**, 685-94.

Packham, J.R. & Cohn, E.V.J. (1990) Ecology of the woodland field layer. *Arboricultural Journal*, **14**, 357-71.

Page, C.N. (1982) *The Ferns of Britain and Ireland*. Cambridge University Press.

Parikesit, P., Larson, D.W. & Matthes-Sears, U. (1996) Impacts of trails on cliff-edge forest structure. *Can. J. Bot.*, **73**, 943-53.

Peace, T.R. & Gilmour, J.S.L. (1949) The effect of picking on the flowering of bluebell, *Scilla non-scripta*. *New Phytologist*, **48**, 115-17.

Pearcy, R.W. & Ward, R.T. (1972) Phenology and growth of Rocky Mountain populations of *Deschampsia cespitosa*. *Ecology*, **53**, 1171-78.

Pearce, T.G. (1984) Earthworm populations in soils disturbed by trampling. *Biological Conservation*, **39**, 172-201.

Poole, T.B. (1959) Studies on the food of Collembola in a Douglas fir plantation. *Proc. Zool. Soc. Lond.*, **132**, 71-82.

Pounder, E.J. (1985) The effects of footpath development on vegetation at the Okstindan research station in arctic Norway. *Biological Conservation*, **34**, 273-88.

Price, M.F. (1985) Impacts of recreational activities on alpine vegetation in western north America. *Mountain Research and Development*, **5**, 263-77.

Pryor, P. (1983) The effects of disturbance on open *Juncus trifidus* heath in the Cairngorm mountains, in R.E.R.G. Report No. 9 (eds N.G.Bayfield & G.C.Barrow), 53-62.

Puri, G.S. (1950) The ecology of the humus layer in some English forests. *Indian Forester*, **76**, 418-27.

Purvis, G. & Curry, J.P. (1980) Successional changes in the Arthropod fauna of a new ley pasture established on previously cultivated arable land. *Journal of Applied Ecology*, **17**, (2), 309-21.

Raunkiaer, C. (1934) *The Life Forms of Plants and Statistical Plant Geography*, Oxford University Press, Oxford.

Ripley, H.T. (1962) *Recreation impact on southern Appalachian campgrounds and picnic sites*. USDA Forest Service, S. East Forest Experimental Station No. 153.

Rodwell, J.S. (1991) *British Plant Communities. I. Woodland and Scrub*. Cambridge University Press, Cambridge.

Rogers, W.S. (1939) Root studies VIII: Apple root growth in relation to rootstock, seasonal and climatic factors. *J. Pomol.*, **17**, 99-130.

Rogova, T.V. (1976) Influence of trampling on vegetation of forest meadows and whortleberry-moss-pine forest cenoses. *Soviet Journal of Ecology*, **7**, 356-9.

Rowell, D.L. (1994) *Soil Science: Methods and Applications*. Longman Scientific & Technical. New York

Rutherford, G.K. & Scott, D.C. (1979) The impact of recreational land use on soil chemistry in a Provincial Park. *Park News*, **5**, 22-25.

Santruckova, H., Heinemeyer, O. & Kaiser, E.A. (1993) The influence of soil compaction on microbial biomass and organic-carbon turnover in microaggregates and macroaggregates. *Geoderma*, **56**, No. 1-4, 587-98.

Schaefer, M. & Schaermann, J. (1990) The soil fauna of beech forests: comparisons between a mull and a moder soil. *Pedobiologia*, **34**, 299-314.

Schofield, J.M. (1978⁶⁷) Human impact on the fauna, flora and natural features of Gibraltar Point, in ^{The biotic effects of public pressures on the environment} ~~The Scientific Management of Animal and Plant Communities for Conservation~~ (eds E. Duffey and A.S. Watt), Blackwell. pp 106-11, NC Parks Wood Symposium No. 3

Schreiner, E.S. (1974) *Vegetation dynamics and human trampling in three subalpine communities of Olympic National Park*. M.Sc. Thesis, University of Washington, Seattle.

- 9
- Schreiner, E.S. & Moorhead, B.B. (1976) Human impact inventory and management in the Olympic National Park backcountry. Conference Proceedings *Recreational Impact on Wildlands*. USDA Forest Service Pacific NW Region, Seattle, Washington, 203-212.
- Scott, J.J. & Kirkpatrick, J.B. (1994) Effects of human trampling on the sub-Antarctic vegetation of Macquarie Island. *Polar Record*, **30**, 207-20.
- Scott-Williams, B.W. (1967) Effects of visitor use on the ecosystems of Rocky Mountain National Park, Colorado, in *Towards a New Relationship of Man and Nature in Temperate Lands. I. Ecological Impact of Recreation and Tourism Upon Temperate Environments*, IUCN No.7, pt. 1.
- Settergren, C.D. & Cole, D.N. (1970) Recreation effects on soil and vegetation in the Missouri Ozarks. *Journal of Forestry*, **68**, 231-3.
- Sidaway, R. (1990) *Birds and Walkers. A Review of Existing Research on Access to the Countryside and Disturbance to Birds*. Ramblers Association.
- Singer, S.W. (1971) *Vegetation response to single and repeated walking stresses in an alpine ecosystem*. M.Sc. Thesis, Rutgers University, NJ.
- Slatter, R.J. (1978) Ecological effects of trampling on sand dune vegetation. *Journal of Biological Education*, **12**, (2), 89-96.
- Slingsby, D. & Cooke, C. (1992) *Practical Ecology*. MacMillan Education Ltd, London.
- Smith, A.J.E. (1978) *The Moss Flora of Britain and Ireland*. Cambridge University Press.
- Smith, R.T. & Atkinson, K. (1975) *Techniques in Pedology*. Unwin Bros.
- Speight, M.C.D. (1973) *Outdoor recreation and its ecological effects. A bibliography and review*. Discussion papers in Conservation No. 4, U.C.L.
- Smeltzer, D.L.K., Bergdahl, D.R. & Donnelly, J.R. (1982) Populations of selected forest soil organisms affected by soil compaction. *American Phytopathological Society NE Division Abstracts*.
- Stalfelt, M.G. (1973) *Plant Ecology: Plants, the soil and man*. Longman, London.

Streeter, D.T. (1971) The effects of public pressure on the vegetation of chalk downlands at Box Hill, Surrey, in *The Scientific Management of Animal and Plant Communities for Conservation*, (Eds E. Duffey and A.S. Watt), 11th BES symposium, Blackwell, Oxford. pp 459-68

Studlar, S.M. (1980) Trampling effects on bryophytes: trail surveys and experiments. *Bryologist*, **83**, 301-13

Studlar, S.M. (1983) Trampling effects on mosses near Mountain Lake, Virginia: Damage and recovery, in *The Ecological Impact of Outdoor Recreation on Mountain Areas in Europe and North America* (eds N.G. Bayfield and G.C. Barrow), Recreation Ecology Research Group Report No. 9, Wye College, England, 182-87.

Sun, D. (1992) Trampling resistance, recovery and growth rate of eight plant species. *Agriculture, Ecosystems and Environment*, **38**, 265-73.

Sun, D. & Liddle, M.J. (1991) Field occurrence, recovery, and simulated trampling resistance and recovery of two grasses. *Biological Conservation*, **57**, 187-203.

Sun, D. & Liddle, M.J. (1993a) A survey of trampling effects on vegetation and soil in eight subtropical and subtropical sites. *Environmental Management*, **17**, No. 4, 497-510.

Sun, D. & Liddle, M.J. (1993b) Plant morphological characteristics and resistance to simulated trampling. *Environmental Management*, **17**, (4), 511-21.

Sun, D. & Liddle, M.J. (1993c) The morphological responses of some Australian tussock grasses and the importance of tiller number in their resistance to trampling. *Biological Conservation*, **65**, (1), 43-49.

Sun, D. & Liddle, M.J. (1993d) Trampling resistance, stem flexibility, and leaf strength in nine Australian grasses and herbs. *Biological Conservation*, **65**, 35-41.

SYSTAT (1992) Version 5.2 Edition. Evanston, IL: SYSTAT, Inc.

Tait, J., Lane, A. & Carr, S. (1988) *Practical Conservation - Site Assessment and Management Planning*. The Open University.

Tansley, A.G. (1953) *The British Isles and their Vegetation*, Cambridge University Press.

- Taylor, K.C., Reader, R.J. & Larson, D.W. (1993) Scale-dependant inconsistencies in the effects of trampling on a forest understorey community. *Environmental Management*, **17**, 239-48.
- Teuben, A. & Smidt, G.R.B. (1992) Soil arthropod numbers and biomass in two pine forests on different soils, related to functional groups. *Pedobiologia*, **36**, 79-89.
- Thomas, R. (1991) *The Ecological Effects of Paintball Games on Ancient Semi-Natural Woodland*. Belham Wood Final Report. English Nature.
- Thompson, P.A. & Cox, S.A. (1978) Germination of the bluebell (*Hyacinthoides non-scripta* (L.) Chouard) in relation to its distribution and habitat. *Ann. Bot.*, **42**, 51-62.
- Thorud, D.B. & Frissell, S.S. (1976) Time changes in soil density following compaction under an oak forest. *Minnesota Forestry Research Notes*, no. 257.
- Tilling, S.M. (1987) A key to the major groups of British terrestrial invertebrates. *Field Studies*, **6**, 697-766.
- Tonnerson, A.S. & Ebersole, J.J. (1997) Human trampling effects on vegetation and age structure of *Pinus edulis* and *Juniperus monosperma*. *Great Basin Naturalist*, **57**, (1), 50-6.
- Wagar, J.A. (1964) *The Carrying Capacity of Wildlands for Recreation*, Forest Science Monograph 7, The Society of American Foresters, Washington, DC.
- Wagar, J.A. (1967) Simulated trampling as a technique in recreation research. IUFRO Congress XIV, Paper VII, Section 26, 239-45.
- Warren, M.S. & Fuller, R.J. (1990) *Woodland Rides and Glades: their Management for Wildlife*. NCC.
- Warren, M.S. & Key, R.S. (1991) Woodlands: Past, present and potential for insects, in *The Conservation of Insects and their Habitats* (eds M. Collins and J.A. Thomas), *Proceedings of the 15th Symposium of the Royal Entomological Society of London*, Academic Press, 155-211.
- Warwick^{SW} District Council (1992) *Crackley Wood - Draft Management Plan*, WDC.
- Watt, A.S. (1976) The ecological status of bracken. *Bot. J. of Lin. Soc.*, **73**, 217-40.

- Weaver, T. & Dale, D. (1978) Trampling effects of hikers, motorcycles and horses in meadows and forests. *Journal of Applied Ecology*, **15**, 451-7.
- Webster, R. & Oliver, M.A. (1990) *Statistical Methods in Soils and Land Resource Survey*, Oxford University Press.
- Webster, S. & Adams, N. (1989) The ecological effects of paintball games on an ancient woodland. *The Planner*, **75**, (6), 11-13.
- Westhoff, V. (1967) The ecological impact of pedestrian, equestrian and vehicular traffic on vegetation, in ~~*Towards a new relationship of man and nature in temperate lands I. Ecological impact of recreation and tourism upon temperate environments for conservation*~~ (Eds E. Duffey and A.S. Watt), 11th BES symposium, Blackwell, Oxford. (UCN No 7, 218-23)
- Whalley, W.R., Dumitru, E. & Dexter, A.R. (1995) Biological effects of soil compaction. *Soil & Tillage Research*, **35**, 53-68.
- Whinam, J. & Comfort, M. (1996) The impact of commercial horse riding on sub-alpine environments at Cradle Mountain, Tasmania. *J. of Env. Mgmt*, **47**, (1), 61-70.
- Whisler, F.D., Engle, C.F. & Baughman, N.M. (1965) *The effects of soil compaction on nitrogen transformations in the soil*. Bulletin, West Virginia University Agricultural Experimental Station, No. 516T.
- Whittaker, R.M. & Likens, C.E. (1975) In *Primary Production of the Biosphere* (eds H. Leita and R.H. Whittaker), Springer Verlag, Berlin 305-28.
- Willard, B.E. & Marr, J.W. (1970) Effects of human activities on alpine tundra ecosystems in Rocky Mountain National Park, Colorado. *Biological Conservation*, **2**, 257-65.
- Willard, B.E. & Marr, J.W. (1971) Recovery of alpine tundra under protection after damage by human activities in the Rocky Mountains of Colorado. *Biological Conservation*, **3**, 181-90.
- Wilson, J.Y. (1959) Vegetative reproduction in the bluebell *Endymion non-scriptus*, *New Phytologist*, **58**, 155-63.
- Wisdom, K.S.F. (1988) *Wildwoods - paintball adventure games in ancient semi-natural woodlands*. M.Sc. Thesis, University College, London.

- Wyatt, N. (1993) *Wildlife Sites in Warwickshire*. Warwickshire Wildlife Trust Report. ,
- Yorks, T.P., West, N.E., Mueller, R.J. & Warren, S.D. (1997) Toleration of traffic by vegetation: Life form conclusions and summary extracts from a comprehensive database. *Environmental Management*, **21**, (1), 121-31.
- Young, R.A. & Gilmore, A.R. (1976) Effects of various camping intensities on soil properties in Illinois campgrounds. *Soil Sci. Soc. Am. J.*, **40**, 908-11.
- Zande, A.N. van der, Berkhuizen, J.C., van Latesteijn, H.C. *et al.* (1984) Impact of outdoor recreation on the density of a number of breeding bird species in woods adjacent to urban residential areas. *Biological Conservation*, **18**, 1-39.
- Zar, J.H. (1984) *Biostatistical Analysis*, 2nd edn, Prentice-Hall International Inc. ,

Appendices¹

Appendix 2.1 Construction of pressure sensitive counter

- *Equipment and construction*

The traditional form of pressure sensitive counter relies on a complicated skeleton of microswitches built into gateways and stiles (Coker & Coker 1972). This new method utilises a moveable pressure sensitive pad connected to an electronic counter hidden nearby. It is not visually obtrusive, is simple and inexpensive to make, it functions well in inclement weather conditions and can be positioned anywhere in a site. It can be used in a wide assortment of scenarios including private and public rural / urban areas, country parks and estates, nature reserves, tourist 'honeypots', school and university grounds and trail systems.

The recording circuit is triggered by a pressure sensitive pad similar to those used for home security systems. The pressure pad is connected to a battery powered electromechanical counter stationed in a weatherproof plastic box, and once activated the count is registered on the display dial. When the pressure pad contacts are depressed, there is a decrease in voltage to the electro-magnet within the counter and this activates the counter dial. Once released, the contacts within the pad separate and the voltage returns so that measuring can continue.

Small multipurpose plastic boxes measuring 10cm x 75 cm x 35cm were drilled to provide a display window for observing the numerical counter, along with some apertures to allow a connection to the pressure pad and the positioning of an on / off switch. The 6-digit electromechanical counter and toggle switch were positioned in their respective holes and fastened in place with clear adhesive applied using a glue gun (this seal also prevented water infiltrating into the box). A length of two core cable was then soldered to connect to the pressure pad itself at one end and also passed into the box to be soldered to the counter and toggle switch at the other end. A

¹ numbering refers to the relevant chapter

9V PP3 battery was soldered to the counter and toggle switch to complete the circuit via a battery snap connector. A toggle switch cover was then added and the battery placed securely in the plastic box which was then sealed by screwing the top on. Some rubber sleeving was then pulled down over the area of exposed soldered wire where the cable connected with the pressure pad and was secured with insulating tape. The unit can then be tested by toggling the circuit 'on' and activating the pad. It is important that the box be adequately waterproofed - a combination of waterproof tape drawn over the box joints and screw-holes, sealed in an air tight clear plastic bag is usually sufficient. The circuit is not effected by changes in the ambient temperature and can withstand moderate to heavy use.

- ***Practical use in the field***

After construction the unit can be taken into the field for implementation in pressure study experiments. One advantage of the system is that it can be positioned anywhere along a path or track as well as at entrances and gateways.

Depending on the dimensions of the pressure pad, a pit can be dug to accomodate the apparatus. Before covering with a thin layer of soil, the pad should be placed in a protective plastic bag and then the pre-dug soil can be added. To prevent detection, the newly disturbed plot can be camouflaged by distributing some leaf litter or topsoil over the surface of the plot, and in only a few days the device will be almost undetectable. The recording unit should be buried a short distance away and hidden. Not only people can be recorded with the apparatus - large mammals such as dogs and deer can also activate the pad.

Coker & Coker (1972) visually calibrated their apparatus and found a 95% success rate. The success rate with this method was 85 %, calibrated using a combination of visual and experimental methods. The calibration result will depend on the size of the pressure pad being used.

- ***List of major components of pressure sensitive counters***

The following are available from: RS Components Ltd, PO Box 253, Duddleston Industrial Estate, Saltley, Birmingham, B8 1BQ.

Item	Reference code	Price (pounds sterling)
Large pressure pad	317-156	4.49 each
Twin miniature PP3 press studs (packs of 100)	489-021	0.22 each
2-core round 2182Y cable (100 M reel)	377-928	0.15 metre
Toggle switches (packs of 5)	350-204	1.17 each
Toggle switch covers (packs of 5)	316-967	0.47 each
2 mm silicone rubber sleeving (10 M reel)	399-445	0.24 metre
Solder (250 g reel)	554-917	7.26
PVC insulating tape (19 mm x 10 M)	494-225	0.44

The following available from: Farnell Electronic Components Ltd, Canal Rd, Leeds, West Yorkshire, LS12 2TU.

Item	Reference code	Price (pounds sterling)
PP3 batteries	MN1604B1	2.86 each
Multipurpose boxes	MB2G	1.54 each
Electromechanical counters	175-791	8.58 each

(NB: All prices include VAT and carriage, and reflect 1994 / 1995 rates).

Appendix 2.2 - Mean plant cover (%), bare ground cover (%), leaf litter cover (%), leaf litter depth (cm), soil penetrative resistance (kg cm⁻²), plant height (cm), visitor numbers (per year), pH, organic matter content (%), soil water content (g H₂O g⁻¹ fresh soil) and light intensity (lux) in the four wear classes at each site and overall for the winter survey with the results of Kruskal-Wallis tests.

Site	Heavy	Moderate	Light	Control	H ^a	p ^b
<i>Overall</i>						
Plant cover %	0.80	9.36	33.30	30.83	77.5	<0.001***
Bare ground %	46.06	18.91	1.35	0.29	77.1	<0.001***
Leaf litter %	53.38	73.97	84.02	94.40	42.3	<0.001***
Leaf litter depth	0.57	0.87	2.82	3.88	80.1	<0.001***
Pen. resistance	3.52	3.56	2.19	1.36	76.2	<0.001***
Plant height	0.14	1.23	9.33	11.61	84.8	<0.001***
Visitor numbers	142	129	36	3	82.2	<0.001***
pH	5.08	5.00	4.64	4.54	14.9	0.002**
Organic matter %	33.03	32.52	31.95	40.93	1.1	0.76
Soil water content	0.475	0.456	0.438	0.467	2.2	0.53
Light intensity	5447	5424	5392	5356	0.2	0.98
<i>Tocil Wood</i>						
Plant cover %	0.94	8.34	25.41	22.91	23.9	<0.001***
Bare ground %	15.94	5.62	2.97	0.78	18.6	<0.001***
Leaf litter %	83.28	88.56	89.22	97.12	13.0	0.005**
Leaf litter depth	0.89	1.32	3.26	3.95	24.3	<0.001***
Pen. resistance	3.87	3.53	2.05	1.23	24.3	<0.001***
Plant height	0.37	1.10	6.14	5.83	24.7	<0.001***
Visitor numbers	99	86	22	4	24.2	<0.001***
pH	5.18	5.11	4.98	5.01	1.0	0.81
Organic matter %	23.49	25.00	17.97	23.62	2.0	0.57
Soil water content	0.407	0.404	0.337	0.398	3.0	0.39
Light intensity	4605	4580	4531	4638	0.1	0.99
<i>Crackley Wood</i>						
Plant cover %	0.25	6.50	30.00	31.94	28.8	<0.001***
Bare ground %	47.50	26.50	0.83	0.00	26.7	<0.001***
Leaf litter %	51.94	74.89	83.97	93.75	13.9	0.003**
Leaf litter depth	0.46	0.59	2.57	3.79	29.1	<0.001***
Pen. resistance	3.46	3.68	2.30	1.46	25.5	<0.001***
Plant height	0.03	1.24	10.10	14.07	29.5	<0.001***
Visitor numbers	106	104	29	2	32.4	<0.001***
pH	4.89	4.79	4.50	4.26	5.0	0.17
Organic matter %	41.98	32.96	29.95	34.25	1.8	0.61
Soil water content	0.546	0.467	0.438	0.452	4.1	0.25
Light intensity	5427	5423	5394	5364	0.1	0.99
<i>Tilehill Wood</i>						
Plant cover %	1.25	13.11	43.53	36.75	24.5	<0.001***
Bare ground %	71.39	23.10	0.42	0.14	31.4	<0.001***
Leaf litter %	28.25	60.08	79.44	92.64	22.3	<0.001***
Leaf litter depth	0.41	0.76	2.67	3.92	28.8	<0.001***
Pen. resistance	3.26	3.47	2.20	1.39	25.9	<0.001***
Plant height	0.05	1.34	11.41	14.28	30.0	<0.001***
Visitor numbers	220	196	57	4	27.2	<0.001***
pH	5.19	5.12	4.48	4.38	10.3	0.016*
Organic matter %	32.57	38.78	46.38	62.98	6.0	0.11
Soil water content	0.464	0.491	0.528	0.601	4.8	0.18
Light intensity	6216	6175	6155	5986	1.1	0.77
H Test^c	Heavy	Moderate	Light	Control		
Plant cover %	3.4 (0.18)	0.7 (0.67)	6.4 (0.041*)	4.5 (0.10)		
Bare ground %	13.9 (<0.001***)	8.4 (0.015*)	0.9 (0.62)	2.7 (0.26)		
Leaf litter %	14.3 (<0.001***)	10.1 (0.006**)	0.2 (0.88)	0.6 (0.75)		
Leaf litter depth	8.3 (0.015*)	11.9 (0.002**)	2.2 (0.33)	0.4 (0.82)		
Pen. resistance	2.0 (0.36)	0.4 (0.80)	0.5 (0.77)	3.1 (0.21)		
Plant height	1.5 (0.47)	0.1 (0.94)	9.7 (0.008**)	12.1 (0.002**)		
Visitor numbers	12.3 (0.002**)	7.6 (0.023*)	3.6 (0.17)	0.03 (0.99)		
pH	1.0 (0.61)	1.6 (0.45)	2.7 (0.26)	6.6 (0.037*)		
Organic matter	2.7 (0.26)	1.1 (0.58)	8.6 (0.013*)	5.9 (0.051)		
Soil water content	6.1 (0.047*)	1.8 (0.41)	9.2 (0.010*)	5.7 (0.056)		
Light intensity	7.3 (0.026*)	7.2 (0.027*)	6.4 (0.041*)	5.6 (0.061)		

^a Kruskal-Wallis H test - between wear classes within each site (Overall df = 399; Crackley & Tocil df = 127; Tilehill df = 143)

^b *** sig. at p ≤ 0.001; ** sig. at p ≤ 0.01; * sig. at p ≤ 0.05

^c Kruskal-Wallis H test - between the three sites (df = 99); probabilities in brackets.

App. 2.3 - Mean plant cover (%), bare ground cover (%), leaf litter cover (%), leaf litter depth (cm), soil penetrative resistance (kg cm⁻²), plant height (cm), visitor numbers (per year), pH, organic matter content (%), soil water content (g H₂O g⁻¹ fresh soil) and light intensity (lux) in the four wear classes at each site and overall for the **spring** survey with the results of Kruskal-Wallis tests.

Site	Heavy	Moderate	Light	Control	H ^a	p ^b
<i>Overall</i>						
Plant cover %	4.81	25.63	73.30	81.00	80.5	<0.001***
Bare ground %	61.77	34.20	4.50	0.90	65.0	<0.001***
Leaf litter %	34.69	49.57	67.90	77.50	29.2	<0.001***
Leaf litter depth	0.42	0.83	2.77	3.60	75.1	<0.001***
Pen. resistance	4.32	3.64	2.32	1.23	79.6	<0.001***
Plant height	0.18	1.74	14.64	19.88	86.3	<0.001***
Visitor numbers	289	183	52	6	82.2	<0.001***
pH	4.87	4.59	4.38	4.25	12.4	0.006**
Organic matter %	33.42	35.52	38.97	51.49	5.7	0.13
Soil water content	0.441	0.432	0.454	0.512	3.7	0.29
Light intensity	7266	7191	7070	6995	0.4	0.94
<i>Tocil Wood</i>						
Plant cover %	10.47	37.75	72.34	89.22	26.4	<0.001***
Bare ground %	22.56	14.37	4.06	1.72	11.0	0.011*
Leaf litter %	66.78	54.44	43.44	41.09	6.8	0.078
Leaf litter depth	0.78	1.49	4.08	4.50	25.0	<0.001***
Pen. resistance	3.80	2.88	2.10	1.10	24.7	<0.001***
Plant height	0.37	2.29	11.36	15.97	27.3	<0.001***
Visitor numbers	230	145	43	7	24.2	<0.001***
pH	5.24	4.98	4.88	4.69	2.4	0.49
Organic matter %	37.08	27.83	26.99	54.67	7.1	0.068
Soil water content	0.557	0.491	0.387	0.558	3.0	0.030*
Light intensity	6412	6644	6388	6559	0.1	0.99
<i>Cruckley Wood</i>						
Plant cover %	1.31	16.06	72.66	79.98	26.4	<0.001***
Bare ground %	71.41	33.90	1.09	0.31	26.7	<0.001***
Leaf litter %	28.75	59.53	77.97	95.31	21.4	<0.001***
Leaf litter depth	0.27	0.55	1.99	3.40	27.7	<0.001***
Pen. resistance	4.80	4.17	2.59	1.50	28.0	<0.001***
Plant height	0.04	1.23	13.93	19.15	28.4	<0.001***
Visitor numbers	309	180	68	5	32.4	<0.001***
pH	4.83	4.71	4.36	4.16	6.0	0.11
Organic matter %	31.16	32.53	37.21	43.50	1.0	0.81
Soil water content	0.389	0.417	0.430	0.472	1.5	0.69
Light intensity	7776	7691	7626	7360	0.4	0.95
<i>Tilehill Wood</i>						
Plant cover %	2.89	23.36	74.72	74.78	29.6	<0.001***
Bare ground %	88.06	52.08	7.92	0.69	30.3	<0.001***
Leaf litter %	11.44	36.39	80.69	94.03	29.2	<0.001***
Leaf litter depth	0.22	0.49	2.29	2.98	28.8	<0.001***
Pen. resistance	4.37	3.85	2.27	1.10	30.3	<0.001***
Plant height	0.14	1.71	18.20	23.99	31.4	<0.001***
Visitor numbers	329	223	46	5	27.2	<0.001***
pH	4.58	4.14	3.95	3.94	11.7	0.0085**
Organic matter %	32.17	45.01	51.18	55.77	3.3	0.35
Soil water content	0.383	0.392	0.534	0.506	4.6	0.20
Light intensity	7776	7691	7626	7360	0.8	0.86
<i>H Test^c</i>						
	Heavy	Moderate	Light	Control		
Plant cover %	2.5 (0.29)	4.1 (0.13)	0.5 (0.79)	8.4 (0.015*)		
Bare ground %	16.0 (<0.001***)	11.4 (0.001**)	5.8 (0.055)	2.5 (0.28)		
Leaf litter %	12.9 (<0.0015**)	5.0 (0.084)	13.1 (0.001***)	6.3 (<0.001***)		
Leaf litter depth	15.3 (<0.001***)	12.7 (0.002**)	13.5 (0.002**)	10.4 (0.0055**)		
Pen. resistance	9.4 (0.0092**)	12.6 (0.0018**)	2.5 (0.29)	13.7 (0.0010**)		
Plant height	3.7 (0.16)	4.5 (0.11)	11.9 (0.003**)	14.4 (<0.001***)		
Visitor numbers	12.3 (0.002**)	7.6 (0.023*)	3.6 (0.17)	0.03 (0.99)		
pH	3.5 (0.17)	6.9 (0.032*)	8.8 (0.012*)	6.1 (0.048*)		
Organic matter	1.2 (0.55)	3.2 (0.20)	3.3 (0.19)	1.0 (0.59)		
Soil water content	6.7 (0.034*)	2.4 (0.30)	2.4 (0.29)	1.1 (0.57)		
Light intensity	3.1 (0.21)	3.8 (0.15)	2.8 (0.24)	2.5 (0.29)		

^a Kruskal-Wallis H test - between wear classes within each site (Overall df = 399; Cruckley & Tocil df = 127; Tilehill df = 143)

^b *** sig. at p ≤ 0.001; ** sig. at p ≤ 0.01; * sig. at p ≤ 0.05

^c Kruskal-Wallis H test - between the three sites (df = 99); probabilities in brackets.

Appendix 2.4 - Mean plant cover (%), bare ground cover (%), leaf litter cover (%), leaf litter depth (cm), soil penetrative resistance (kg cm⁻²), plant height (cm), visitor numbers (per year), pH, organic matter content (%), soil water content (g H₂O g⁻¹ fresh soil) and light intensity (lux) in the four wear classes at each site and overall for the **summer** survey with the results of Kruskal-Wallis tests.

Site	Heavy	Moderate	Light	Control	H ^a	p ^b
<i>Overall</i>						
Plant cover %	6.41	33.89	76.39	86.59	78.1	<0.001***
Bare ground %	74.25	37.03	6.51	0.45	78.9	<0.001***
Leaf litter %	23.39	48.15	72.31	94.79	64.5	<0.001***
Leaf litter depth	0.28	0.68	1.99	3.47	74.8	<0.001***
Pen. resistance	4.98	4.68	2.91	1.74	84.5	<0.001***
Plant height	0.29	6.20	23.66	44.75	83.7	<0.001***
Visitor numbers	838	505	111	16	82.2	<0.001***
pH	4.87	4.83	4.48	4.32	20.6	0.001**
Organic matter %	18.68	22.73	30.39	38.04	25.2	<0.001***
Soil water content	0.212	0.239	0.297	0.315	12.6	0.0056**
Light intensity	8638	8350	7460	5674	13.5	0.0036**
<i>Tocil Wood</i>						
Plant cover %	6.97	32.37	61.69	88.59	26.1	<0.001***
Bare ground %	53.81	22.28	2.50	0.31	24.0	<0.001***
Leaf litter %	44.19	70.62	85.59	92.03	16.3	0.001**
Leaf litter depth	0.53	1.27	2.70	4.84	28.7	<0.001***
Pen. resistance	4.84	4.42	3.18	1.88	26.5	<0.001***
Plant height	0.25	2.03	20.34	41.15	25.6	<0.001***
Visitor numbers	476	267	75	14	24.2	<0.001***
pH	5.31	5.21	4.93	4.79	13.5	0.004**
Organic matter %	17.22	19.57	18.56	22.61	2.9	0.41
Soil water content	0.176	0.162	0.189	0.244	5.0	0.17
Light intensity	7633	7273	6768	5112	3.0	0.39
<i>Crackley Wood</i>						
Plant cover %	3.94	21.37	76.71	82.66	25.3	<0.001***
Bare ground %	79.06	50.94	4.72	0.16	26.8	<0.001***
Leaf litter %	18.91	39.22	77.62	97.50	26.4	<0.001***
Leaf litter depth	0.24	0.45	1.36	3.10	27.5	<0.001***
Pen. resistance	5.04	4.85	2.46	1.31	27.8	<0.001***
Plant height	0.21	3.34	24.90	42.74	27.2	<0.001***
Visitor numbers	994	577	141	16	28.7	<0.001***
pH	4.62	4.74	4.33	4.16	7.5	0.057
Organic matter %	15.21	23.06	32.41	46.80	17.6	<0.001***
Soil water content	0.232	0.302	0.389	0.354	5.1	0.16
Light intensity	7603	7291	6593	5454	2.5	0.48
<i>Tilehill Wood</i>						
Plant cover %	8.11	46.36	89.17	88.30	28.5	<0.001***
Bare ground %	88.14	37.78	11.67	0.83	30.5	<0.001***
Leaf litter %	8.89	36.11	55.28	94.83	27.0	<0.001***
Leaf litter depth	0.10	0.37	1.94	2.58	29.8	<0.001***
Pen. resistance	5.06	4.76	3.07	1.99	31.0	<0.001***
Plant height	0.39	6.17	25.51	48.92	29.1	<0.001***
Visitor numbers	1045	672	117	17	30.9	<0.001***
pH	4.71	4.58	4.20	4.03	26.3	<0.001***
Organic matter %	23.06	25.24	39.12	43.98	16.7	<0.001***
Soil water content	0.227	0.251	0.311	0.343	6.2	0.10
Light intensity	10451	10247	8846	6367	17.7	<0.001***
<i>H Test^c</i>						
	Heavy	Moderate	Light	Control		
Plant cover %	3.2 (0.20)	6.9 (0.031*)	8.9 (0.011*)	1.5 (0.47)		
Bare ground %	7.2 (0.027*)	5.9 (0.051)	5.8 (0.055)	0.5 (0.77)		
Leaf litter %	9.6 (<0.008**)	9.3 (0.009**)	8.4 (0.015*)	1.2 (55)		
Leaf litter depth	16.1 (<0.001***)	16.2 (<0.001***)	12.4 (0.002**)	16.3 (<0.001***)		
Pen. resistance	4.7 (0.093)	3.8 (0.15)	5.2 (0.074)	12.8 (0.002**)		
Plant height	4.6 (0.10)	1.9 (0.38)	1.7 (0.43)	0.01 (0.99)		
Visitor numbers	11.6 (0.002**)	7.5 (0.023*)	2.8 (0.25)	0.01 (0.99)		
pH	12.5 (0.002**)	8.9 (0.011*)	12.7 (0.002**)	12.1 (0.002**)		
Organic matter	5.2 (0.07)	2.0 (0.36)	9.8 (0.007**)	14.8 (<0.001***)		
Soil water content	1.3 (0.52)	6.4 (0.041*)	7.2 (0.027*)	4.9 (0.085)		
Light intensity	4.8 (0.09)	3.7 (0.16)	3.7 (0.16)	1.8 (0.40)		

^a Kruskal-Wallis H test - between wear classes within each site (Overall df = 399; Crackley & Tocil df = 127; Tilehill df = 143)

^b *** sig. at p ≤ 0.001; ** sig. at p ≤ 0.01; * sig. at p ≤ 0.05

^c Kruskal-Wallis H test - between the three sites (df = 99); probabilities in brackets.

Appendix 2.5 - Mean plant cover (%), bare ground cover (%), leaf litter cover (%), leaf litter depth (cm), soil penetrative resistance (kg cm⁻²), plant height (cm), visitor numbers (per year), pH, organic matter content (%), soil water content (g H₂O g⁻¹ fresh soil) and light intensity (lux) in the four wear classes at each site and overall for the **autumn** survey with the results of Kruskal-Wallis tests.

Site	Heavy	Moderate	Light	Control	H ^a	p ^b
<i>Overall</i>						
Plant cover %	2.57	22.07	53.83	57.04	71.8	<0.001***
Bare ground %	34.27	12.45	1.63	0.36	59.0	<0.001***
Leaf litter %	64.83	76.14	83.78	95.17	33.1	<0.001***
Leaf litter depth	0.91	1.55	3.10	4.58	67.6	<0.001***
Pen. resistance	4.53	4.11	2.45	1.47	73.3	<0.001***
Plant height	0.19	2.69	16.26	30.65	79.8	<0.001***
Visitor numbers	614	357	94	12	82.2	<0.001***
pH	4.90	4.77	4.46	4.45	9.2	0.026*
Organic matter %	24.49	26.83	37.69	44.32	7.1	0.049*
Soil water content	0.391	0.398	0.425	0.473	3.1	0.37
Light intensity	6549	6473	6377	6197	1.0	0.81
<i>Tocil Wood</i>						
Plant cover %	2.31	17.16	47.50	53.03	25.4	<0.001***
Bare ground %	36.09	15.78	2.03	0.47	24.5	<0.001***
Leaf litter %	63.97	79.50	91.12	97.37	18.3	<0.001***
Leaf litter depth	1.35	1.84	3.35	4.87	22.2	<0.001***
Pen. resistance	4.82	4.19	2.68	1.74	25.1	<0.001***
Plant height	0.23	2.81	12.58	31.64	25.9	<0.001***
Visitor numbers	387	197	67	11	24.2	<0.001***
pH	5.39	5.20	5.04	4.93	3.2	0.35
Organic matter %	19.47	17.17	16.30	16.16	0.7	0.86
Soil water content	0.298	0.271	0.248	0.251	0.9	0.82
Light intensity	5657	5587	5476	5454	0.05	0.99
<i>Crackley Wood</i>						
Plant cover %	0.89	12.43	43.32	43.89	22.7	<0.001***
Bare ground %	21.43	7.50	0.36	0.36	13.3	0.0040**
Leaf litter %	78.57	89.96	96.25	95.18	7.6	0.054
Leaf litter depth	0.67	1.33	3.65	3.44	22.5	<0.001***
Pen. resistance	4.44	4.45	2.26	1.62	21.3	<0.001***
Plant height	0.47	1.40	11.74	13.25	22.9	<0.001***
Visitor numbers	847	490	135	14	23.2	<0.001***
pH	4.36	4.30	4.10	4.01	5.2	0.16
Organic matter %	24.50	28.97	51.46	60.17	15.1	0.0073**
Soil water content	0.462	0.473	0.550	0.622	6.7	0.082
Light intensity	6921	6829	6714	6693	0.2	0.97
<i>Tilehill Wood</i>						
Plant cover %	4.11	33.94	67.64	70.83	26.5	<0.001***
Bare ground %	42.64	13.33	2.28	0.28	22.2	<0.001***
Leaf litter %	54.92	62.42	67.56	93.19	12.6	0.0055**
Leaf litter depth	0.72	1.46	2.46	5.21	26.8	<0.001***
Pen. resistance	4.33	3.78	2.38	1.13	26.8	<0.001***
Plant height	0.27	3.57	23.05	43.30	32.2	<0.001***
Visitor numbers	608	385	81	10	30.9	<0.001***
pH	4.88	4.74	4.23	4.37	7.3	0.062
Organic matter %	28.95	33.75	45.99	57.03	6.0	0.11
Soil water content	0.418	0.454	0.485	0.554	3.9	0.28
Light intensity	7053	6983	6917	6472	2.8	0.42
<i>H Test^c</i>						
	Heavy	Moderate	Light	Control		
Plant cover %	3.7 (0.16)	12.3 (0.0022**)	12.2 (0.0022**)	13.7 (0.0010**)		
Bare ground %	2.9 (0.23)	2.9 (0.23)	3.2 (0.20)	0.5 (0.79)		
Leaf litter %	2.9 (0.24)	7.0 (0.030*)	4.9 (0.087)	1.9 (0.38)		
Leaf litter depth	8.2 (0.017*)	3.1 (0.21)	4.7 (0.095)	5.1 (0.077)		
Pen. resistance	4.5 (0.11)	4.2 (0.12)	1.5 (0.47)	8.5 (0.014*)		
Plant height	3.8 (0.15)	4.6 (0.10)	10.3 (0.0057**)	10.1 (0.006**)		
Visitor numbers	11.0 (0.004**)	7.1 (0.028*)	4.1 (0.13)	0.1 (0.96)		
pH	12.1 (0.0024**)	8.7 (0.013*)	10.4 (0.0056**)	9.1 (0.011*)		
Organic matter	3.8 (0.15)	2.8 (0.25)	11.7 (0.0029**)	10.7 (0.0047**)		
Soil water content	12.1 (0.002**)	9.1 (0.011*)	12.0 (0.0025**)	13.8 (0.001**)		
Light intensity	3.7 (0.16)	4.8 (0.089)	5.0 (0.081)	3.2 (0.20)		

^a Kruskal-Wallis H test - between wear classes within each site (*Overall* df = 399; *Crackley & Tocil* df = 127; *Tilehill* df = 143)

^b *** sig. at p ≤ 0.001; ** sig. at p ≤ 0.01; * sig. at p ≤ 0.05

^c Kruskal-Wallis H test - between the three sites (df = 99); probabilities in brackets.

Appendix 2.6 - Mean plant cover (%), frequency (%), height (cm), leaf length (cm) and leaf width (cm)^a in each wear class combined for all three sites in the **winter** survey with the results of statistical tests.

Species	Heavily trampled	Moderately trampled	Lightly trampled	Control untrampled	H or U ^b	p
<i>Poa</i> spp. ^c						
FR:	10	26	8	-		
CO:	3.8	6.6	6.0	-	2.0	0.36
HT:	1.4	3.1	6.9	-	18.6	<0.001***
LL:	2.3	4.4	6.5	-	12.6	0.0018**
LW:	0.2	0.3	0.3	-	4.7	0.096
<i>Eurynchium praelongum</i>						
FR:	4	13	17	9		
CO:	5.7	11.9	10.1	11.8	4.8	0.19
<i>Deschampsia cespitosa</i>						
FR:	1	9	17	12		
CO:	8.0	10.2	19.9	20.2	9.2	0.027
HT:	1.2	5.1	14.8	19.7	17.9	<0.001***
LL:	3.7	8.1	17.0	22.5	17.2	<0.001***
LW:	0.2	0.4	0.4	0.4	4.0	0.26
<i>Geum urbanum</i>						
FR:	1	1	5	5		
CO:	5.0	7.0	8.6	12.0		
HT:	0.8	2.5	6.4	6.7		
LL:	1.3	2.4	3.6	3.7		
LW:	1.2	3.1	4.6	5.2		
<i>Lolium perenne</i>						
FR:	1	2	2	-		
CO:	3.0	17.5	10.0	-		
HT:	1.0	3.2	11.5	-		
LL:	1.9	4.2	12.5	-		
LW:	0.1	0.2	0.4	--		
<i>Dicranum</i> spp						
FR:	1	1	1	-		
CO:	3.0	5.0	5.0	-		
<i>Holcus</i> spp. ^d						
FR:	-	16	28	10		
CO:	-	5.9	8.1	7.5	3.1	0.21
HT:	-	3.0	8.3	7.7	22.3	<0.001***
LL:	-	4.8	8.8	9.5	25.6	<0.001***
LW:	-	0.3	0.4	0.4	1.7	0.45
<i>Hedera helix</i>						
FR:	-	10	14	20		
CO:	-	5.0	9.4	8.7	6.5	0.039*
HT:	-	2.6	5.7	6.5	15.9	<0.001***
LL:	-	1.9	3.3	3.5	12.1	0.0023**
LW:	-	2.0	3.9	4.2	13.3	0.0013**
<i>Rubus fruticosus</i> agg.						
FR:	-	7	61	63		
CO:	-	6.4	15.4	18.6	14.3	<0.001***
HT:	-	3.3	20.7	25.2	23.4	<0.001***
LL:	-	4.4	6.5	7.1	13.5	0.0012**
LW:	-	2.9	4.5	5.1	10.0	0.001**
<i>Thuidium tamariscinum</i>						
FR:	-	5	4	6		
CO:	-	4.6	20.0	14.0	5.9	0.053
<i>Gulium aparine</i>						
FR:	-	4	5	6		
CO:	-	2.2	9.0	7.1	1.5	0.47
HT:	-	2.7	6.1	6.1	6.9	0.030*
LL:	-	0.4	0.4	0.5	0.9	0.64
LW:	-	0.3	0.3	0.3	1.7	0.42
<i>Taraxacum officinales</i>						
FR:	-	3	2	-		
CO:	-	6.0	15.0	-		
HT:	-	3.4	5.5	-		
LL:	-	4.2	7.5	-		
LW:	-	1.4	2.6	-		
<i>Pseudoscleropodium purum</i>						
FR:	-	3	1	1		
CO:	-	21.7	10.0	10.0		
<i>Silene dioica</i>						
FR:	-	2	4	6		
CO:	-	5.0	13.2	22.5	4.1	0.13
HT:	-	2.7	3.7	12.1	8.1	0.017*
LL:	-	2.8	5.4	7.3	4.5	0.10
LW:	-	1.7	2.2	3.4	6.2	0.045*
<i>Carex</i> spp.						
FR:	-	2	4	-		
CO:	-	4.0	13.2	-		
HT:	-	2.3	13.2	-		
LL:	-	4.7	14.4	-		
LW:	-	0.4	0.8	-		
<i>Ranunculus ficaria</i>						
FR:	-	2	3	1		
CO:	-	6.0	6.0	9.0		
HT:	-	4.0	5.3	10.0		
LL:	-	1.2	2.3	2.5		
LW:	-	1.0	2.1	2.2		

Species	Heavily trampled	Moderately trampled	Lightly trampled	Control untrampled	H or U ^b	p
<i>Stellaria media</i>						
FR:	-	2	3	-		
CO:	-	3.0	11.7	-		
HT:	-	1.2	3.0	-		
LL:	-	0.3	0.4	-		
LW:	-	0.3	0.3	-		
<i>Plagiomnium undulatum</i>						
FR:	-	2	2	2		
CO:	-	5.5	32.5	12.5		
<i>Juncus spp.</i>						
FR:	-	2	6	-		
CO:	-	11.5	14.2	-		
HT:	-	5.7	20.3	-		
LL:	-	17.5	24.5	-		
LW:	-	0.2	0.3	-		
<i>Glechoma hederacea</i>						
FR:	-	1	2	2		
CO:	-	2.0	10.0	14.0		
HT:	-	1.0	6.5	6.9		
LL:	-	0.5	2.3	2.0		
LW:	-	0.8	2.5	2.0		
<i>Anthriscus sylvestris</i>						
FR:	-	1	3	1		
CO:	-	6.0	10.0	15.0		
HT:	-	4.0	6.2	13.0		
<i>Galeobdolon luteum</i>						
FR:	-	1	2	-		
CO:	-	10.0	13.5	-		
HT:	-	3.5	7.2	-		
LL:	-	4.5	2.5	-		
LW:	-	2.4	2.0	-		
<i>Deschampsia flexuosa</i>						
FR:	-	1	4	3		
CO:	-	10.0	21.2	16.7		
HT:	-	2.5	10.7	9.3		
LL:	-	5.7	14.0	12.7		
LW:	-	0.1	0.1	0.1		
<i>Urtica dioica</i>						
FR:	-	-	2	4		
CO:	-	-	5.0	6.5		
HT:	-	-	6.6	7.1		
LL:	-	-	1.2	2.3		
LW:	-	-	0.8	1.7		
<i>Alliaria petiolata</i>						
FR:	-	-	1	2		
CO:	-	-	15.0	7.5		
HT:	-	-	6.5	7.5		
LL:	-	-	4.0	3.7		
LW:	-	-	4.5	3.0		
<i>Arum maculatum</i>						
FR:	-	-	2	1		
CO:	-	-	19.0	10.0		
HT:	-	-	9.0	8.0		
LL:	-	-	7.0	8.0		
LW:	-	-	3.8	3.0		
<i>Mercurialis perennis</i>						
FR:	-	-	1	5		
CO:	-	-	8.0	9.8		
HT:	-	-	4.5	7.7		
LL:	-	-	7.0	7.2		
LW:	-	-	3.3	3.2		
<i>Stellaria holostea</i>						
FR:	-	-	1	4		
CO:	-	-	15.0	8.2		
HT:	-	-	6.0	11.2		
LL:	-	-	2.0	2.0		
LW:	-	-	0.3	0.3		
<i>Brachythecium rutabulum</i>						
FR:	-	-	2	4		
CO:	-	-	12.5	11.2		
<i>Mnium hornum</i>						
FR:	-	-	1	3		
CO:	-	-	5.0	6.7		
<i>Dryopteris filix-mas</i>						
FR:	-	-	2	7		
CO:	-	-	8.0	13.1		
HT:	-	-	12.0	23.4		
<i>Brachypodium sylvaticum</i>						
FR:	-	-	7	3		
CO:	-	-	11.6	8.3		
HT:	-	-	12.1	10.5		
LL:	-	-	12.6	14.3		
LW:	-	-	1.0	1.3		
<i>Polytrichum spp.</i>						
FR:	-	-	1	1		
CO:	-	-	30.0	20.0		
<i>Plagiomnium undulatum</i>						
FR:	-	-	2	4		
CO:	-	-	4.0	9.9		
<i>Hyacinthoides non-scripta</i>						
FR:	-	-	2	6		
CO:	-	-	4.0	3.8		
HT:	-	-	3.7	3.0		
LL:	-	-	3.7	3.0		
LW:	-	-	0.8	0.7		
<i>Lonicera periclymenum</i>						

Species	Heavily trampled	Moderately trampled	Lightly trampled	Control untrampled	H or U ^b	p
FR:	-	-	8	13		
CO:	-	-	6.6	9.4	36.5	0.21
HT:	-	-	16.7	18.6	58.5	0.64
LL:	-	-	2.1	3.3	23.0	0.035*
LW:	-	-	1.2	1.3	4.0	0.42
<i>Dryopteris dilatata</i>						
FR:	-	-	2	5		
CO:	-	-	7.5	16.0		
HT:	-	-	10.5	16.0		
<i>Digitalis purpurea</i>						
FR:	-	-	5	2		
CO:	-	-	22.0	25.0		
HT:	-	-	7.2	6.9		
LL:	-	-	14.1	18.0		
LW:	-	-	8.4	9.5		
<i>Viola riviniana</i>						
FR:	-	-	1	2		
CO:	-	-	30.0	9.0		
HT:	-	-	6.0	7.4		
LL:	-	-	2.2	2.2		
LW:	-	-	2.2	2.0		
<i>Dactylis glomerata</i>						
FR:	-	-	1	1		
CO:	-	-	20.0	15.0		
HT:	-	-	3.0	10.0		
LL:	-	-	10.0	12.0		
LW:	-	-	0.3	0.4		
<i>Dryopteris affinis</i>						
FR:	-	-	1	2		
CO:	-	-	20.0	22.5		
HT:	-	-	12.0	20.5		
<i>Ilex aquifolium</i> ^e						
FR:	-	-	5	10		
CO:	-	-	15.0	15.0	23.5	0.84
HT:	-	-	18.7	27.6	17.0	0.33
LL:	-	-	6.4	5.3	32.0	0.39
LW:	-	-	2.1	2.6	16.0	0.27

Species found in only one wear class (m = moderately trampled, l = lightly trampled, c = control)

	Wear class	FR	CO	HT	LL	LW
<i>Leucobryum glaucum</i>	m	2	4.0	-	-	-
<i>Veronica chamaedrys</i>	m	2	12.5	2.0	0.4	0.5
<i>V. montana</i>	m	1	4.0	3.5	1.8	1.0
<i>Rumex sanguineus</i>	m	1	7.0	2.4	4.5	2.0
<i>Ranunculus acris</i>	m	1	5.0	3.0	1.0	0.8
<i>Cardamine pratensis</i>	m	1	4.0	1.0	0.4	0.33
<i>Rumex obtusifolius</i>	l	1	30.0	7.5	4.0	2.2
<i>Vicia sepium</i>	l	1	2.0	10.0	-	-
<i>Lysimachia nummularia</i>	l	1	20.0	5.0	4.0	2.2
<i>Epilobium</i> spp.	l	1	5.0	4.0	1.9	0.8
<i>Oxalis acetosella</i>	l	1	5.0	3.0	0.7	1.2
<i>Rhytidadelphus triquestris</i>	l	2	4.5	-	-	-
<i>Hylocomium splendens</i>	c	1	10.0	-	-	-

Total species frequency 6 29 50 36

^a - FR = percent frequency (number of quadrats containing the species divided by the total number of quadrats); CO = vegetation cover (%); PH = plant height (cm); LL = leaf length (cm); LW = leaf width (cm) (all expressed as total mean divided by species frequency)

^b - Kruskal-Wallis 'H' statistic for data set comparing 3 or more wear classes; Mann Whitney 'U' statistic for comparing 2 wear classes; *** sig. at p ≤ 0.001; ** sig. at p ≤ 0.01; * sig. at p ≤ 0.05

^c - mix of *Poa annua* and *P. pratensis*

^d - mix of *Holcus mollis* and *H. lanatus*

^e - sapling / seedling

Appendix 2.7 - Mean plant cover (%), frequency (%), height (cm), leaf length (cm) and leaf width (cm)^a in each wear class combined for all three sites in the spring survey with the results of statistical tests.

Species	Heavily trampled	Moderately trampled	Lightly trampled	Control untrampled	H or U ^b	p
<i>Poa</i> spp. ^c						
FR:	18	38	6	-		
CO:	4.7	12.8	14.2	-	22.6	<0.001***
HT:	0.9	2.1	8.1	-	32.6	<0.001***
LL:	1.9	3.2	7.8	-	26.2	<0.001***
LW:	0.2	0.2	0.3	-	16.5	<0.001***
<i>Eurynchium praelongum</i>						
FR:	12	21	6	9		
CO:	9.8	8.3	10.0	10.8	1.9	0.60
<i>Hyacinthoides non-scripta</i>						
FR:	11	31	42	45		
CO:	4.4	11.5	38.0	54.5	75.0	<0.001***
HT:	3.4	4.3	15.6	21.6	98.5	<0.001***
LL:	3.7	6.5	18.9	24.5	94.5	<0.001***
LW:	0.5	0.5	0.9	1.1	85.3	<0.001***
<i>Anemone nemorosa</i>						
FR:	7	11	28	25		
CO:	4.7	5.4	16.9	25.0	31.77	<0.001***
HT:	1.8	3.3	10.5	14.0	46.7	<0.001***
LL:	1.1	1.4	3.3	3.8	38.4	<0.001***
LW:	0.6	0.9	1.5	1.8	28.4	<0.001****
<i>Holcus</i> spp. ^d						
FR:	5	14	25	9		
CO:	9.4	9.7	17.8	15.2	9.7	0.021*
HT:	1.9	3.7	15.9	21.2	34.7	<0.001***
LL:	3.9	4.9	14.5	17.2	33.3	<0.001***
LW:	0.2	0.3	0.5	0.5	20.9	<0.001***
<i>Plantago major</i>						
FR:	5	10	-	-		
CO:	6.8	10.2	-	-	23.0	0.80
HT:	1.2	2.1	-	-	8.0	0.035*
LL:	2.3	3.5	-	-	10.5	0.075
LW:	1.6	2.3	-	-	12.5	0.12
<i>Deschampsia cespitosa</i>						
FR:	4	10	17	2		
CO:	13.5	18.4	31.2	20.0	3.1	0.374
HT:	5.9	7.9	20.6	23.0	20.6	<0.001***
LL:	7.5	9.8	24.4	24.0	20.0	<0.001***
LW:	0.2	0.2	0.3	0.3	10.5	0.014*
<i>Ranunculus ficaria</i>						
FR:	2	5	8	10		
CO:	12.0	8.4	18.7	10.5	3.8	0.28
HT:	1.2	2.0	5.9	9.4	15.4	0.0015**
LL:	1.2	1.3	2.4	2.9	14.3	0.0025**
LW:	1.5	1.3	2.2	3.3	13.0	0.0047**
<i>Stellaria holostea</i>						
FR:	2	1	5	3		
CO:	2.0	5.0	11.0	5.0	8.0	0.045*
HT:	5.5	6.5	19.1	11.2	5.0	0.177
LL:	2.8	3.0	4.0	3.7	2.5	0.48
LW:	0.3	0.4	0.5	0.4	2.5	0.467
<i>Taraxacum officinales</i>						
FR:	2	5	6	2		
CO:	12.5	9.6	15.8	17.5	2.6	0.46
HT:	2.3	1.8	11.7	18.0	10.3	0.016*
LL:	6.2	5.7	13.7	19.0	9.1	0.028*
LW:	1.6	1.9	3.3	5.2	9.1	0.028*
<i>Glechoma hederacea</i>						
FR:	1	3	5	3		
CO:	3.0	9.0	8.6	11.0	2.8	0.43
HT:	1.8	3.2	8.4	11.0	6.5	0.089
LL:	1.0	1.2	3.4	2.6	7.8	0.049*
LW:	1.2	1.6	3.6	2.8	6.5	0.091
<i>Hedera helix</i>						
FR:	1	13	16	31		
CO:	4.0	5.1	7.4	9.7	9.2	0.026*
HT:	1.9	3.6	6.6	7.9	25.3	<0.001***
LL:	2.0	2.8	3.8	4.1	11.8	0.008**
LW:	1.8	3.2	4.3	4.8	11.4	0.0098**
<i>Silene dioica</i>						
FR:	1	7	7	2		
CO:	10.0	9.9	15.7	12.5	0.4	0.94
HT:	2.2	4.4	8.9	9.7	6.7	0.082
LL:	4.8	3.7	5.8	7.0	4.2	0.24
LW:	2.2	2.2	3.0	3.1	2.8	0.43
<i>Galium aparine</i>						
FR:	1	4	14	11		
CO:	4.0	3.5	4.9	10.3	5.0	0.13
HT:	1.6	2.3	10.1	14.2	13.4	0.0038**
LL:	0.3	0.6	1.2	1.1	7.2	0.066
LW:	0.1	0.3	0.3	0.3	10.5	0.014*
<i>Plagiomnium undulatum</i>						
FR:	1	1	1	1		
CO:	4.0	5.0	10.0	10.0		

Species	Heavily trampled	Moderately trampled	Lightly trampled	Control untrampled	H or U ^b	p
<i>Acer pseudoplatanus</i> ^c						
FR:	1	6	3	1		
CO:	2.0	2.5	3.3	2.0		
HT:	3.0	4.0	5.7	8.0		
LL:	4.0	3.0	3.9	4.0		
LW:	0.9	0.6	0.9	0.9		
<i>Stellaria media</i>						
FR:	1	5	2	-		
CO:	2.0	5.4	17.5	-		
HT:	0.5	1.7	5.5	-		
LL:	0.3	0.5	0.6	-		
LW:	0.2	0.4	0.4	-		
<i>Geum urbanum</i>						
FR:	-	7	14	4		
CO:	-	14.4	13.7	9.5	0.8	0.66
HT:	-	3.7	8.8	15.0	13.2	0.0014**
LL:	-	2.6	3.7	5.8	12.2	0.0023**
LW:	-	2.4	4.7	6.9	13.1	0.0014**
<i>Rubus fruticosus</i> agg.						
FR:	-	8	38	49		0.0049**
CO:	-	9.0	23.5	26.4	10.6	<0.001***
HT:	-	8.2	20.7	24.2	17.6	0.016*
LL:	-	4.4	5.0	5.9	8.2	0.041*
LW:	-	3.3	3.6	4.1	6.4	
<i>Oxalis acetosella</i>						
FR:	-	3	14	4		
CO:	-	6.0	11.1	12.0	1.7	0.43
HT:	-	2.9	5.3	5.8	3.5	0.17
LL:	-	1.0	1.5	1.6	3.5	0.17
LW:	-	1.2	1.7	2.1	4.9	0.087
<i>Mnium hornum</i>						
FR:	-	3	4	5		
CO:	-	10.0	12.6	8.6		
<i>Rumex sanguineus</i>						
FR:	-	3	2	1		
CO:	-	7.0	9.0	40.0		
HT:	-	2.5	7.0	20.0		
LL:	-	6.1	9.2	7.5		
LW:	-	3.0	3.4	2.5		
<i>Brachypodium sylvaticum</i>						
FR:	-	3	5	2		0.20
CO:	-	12.7	9.2	12.5	3.2	0.083
HT:	-	9.8	8.9	18.0	4.9	0.48
LL:	-	12.2	12.6	13.0	1.5	0.035*
LW:	-	0.3	0.6	0.9	6.7	
<i>Juncus</i> spp.						
FR:	-	3	5	1		
CO:	-	15.0	20.0	20.0		
HT:	-	10.0	34.2	34.0		
LL:	-	11.3	34.2	34.0		
LW:	-	0.3	0.3	0.3		
<i>Ranunculus acris</i>						
FR:	-	4	1	2		
CO:	-	7.5	60.0	12.5		
HT:	-	1.8	18.0	10.5		
LL:	-	1.8	4.5	3.7		
LW:	-	2.0	3.5	4.6		
<i>Veronica hederifolia</i>						
FR:	-	2	2	2		
CO:	-	4.0	6.5	5.5		
HT:	-	2.1	4.1	5.6		
LL:	-	1.5	1.9	2.4		
LW:	-	1.2	1.5	1.9		
<i>Bromus ramosus</i>						
FR:	-	2	4	5		0.27
CO:	-	6.5	15.2	21.0	2.6	0.15
HT:	-	4.7	20.2	23.6	3.7	0.20
LL:	-	9.1	17.0	19.0	3.2	0.071
LW:	-	0.4	1.0	1.1	5.3	
<i>Digitalis purpurea</i>						
FR:	-	2	7	2		0.50
CO:	-	17.5	27.9	32.5	1.4	0.049*
HT:	-	5.5	16.7	21.0	6.0	0.087
LL:	-	5.1	10.9	15.5	4.9	0.080
LW:	-	2.5	5.8	7.2	5.0	
<i>Arum maculatum</i>						
FR:	-	1	4	8		0.23
CO:	-	10.0	15.0	18.0	2.9	0.016
HT:	-	10.0	12.7	18.6	8.2	0.14
LL:	-	9.4	10.4	13.4	3.9	0.11
LW:	-	4.6	6.1	7.5	4.5	
<i>Polystichum</i> spp.						
FR:	-	1	3	-		
CO:	-	5.0	11.7	-		
<i>Galeobdolon luteum</i>						
FR:	-	1	2	1		
CO:	-	4.0	24.0	20.0		
HT:	-	3.5	10.3	13.5		
LL:	-	2.8	4.0	4.3		
LW:	-	1.4	2.3	2.3		
<i>Anthriscus sylvestris</i>						
FR:	-	1	1	3		
CO:	-	6.0	8.0	10.3		
HT:	-	3.1	7.9	12.0		
<i>Conopodium majus</i>						
FR:	-	1	1	2		

Species	Heavily trampled	Moderately trampled	Lightly trampled	Control untrampled	H or U ^b	p
CO:	-	5.0	10.0	4.5		
HT:	-	3.4	11.0	6.6		
LL:	-	0.5	0.7	0.6		
LW:	-	0.2	0.6	0.2		
<i>Sorbus aucuparia</i> ^e						
FR:	-	1	3	6		
CO:	-	7.0	20.0	24.2	2.6	0.28
HT:	-	4.0	22.2	35.5	3.8	0.15
LL:	-	1.6	1.5	1.8	0.9	0.64
LW:	-	1.2	0.8	1.0	1.2	0.56
<i>Leucobryum glaucum</i>						
FR:	-	2	1	3		
CO:	-	7.5	10.0	7.0		
<i>Hypnum cupressiforme</i>						
FR:	-	1	1	-		
CO:	-	5.0	5.0	-		
<i>Dactylis glomerata</i>						
FR:	-	1	4	6		
CO:	-	10.0	17.5	13.7	5.7	0.059
HT:	-	7.5	19.5	16.5	7.4	0.025*
LL:	-	9.0	17.1	19.2	5.4	0.068
LW:	-	0.2	0.4	0.4	1.6	0.451
<i>Heracleum sphondylium</i>						
FR:	-	1	1	1		
CO:	-	10.0	40.0	50.0		
HT:	-	6.0	41.0	50.0		
LL:	-	4.0	20.0	13.0		
LW:	-	5.0	14.0	21.0		
<i>Plagiomnium undulatum</i>						
FR:	-	1	2	2		
CO:	-	5.0	30.0	12.5		
<i>Pseudoscleropodium purum</i>						
FR:	-	1	1	1		
CO:	-	20.0	20.0	25.0		
<i>Rumex obtusifolius</i>						
FR:	-	2	3	-		
CO:	-	7.5	14.0	-		
HT:	-	2.0	9.1	-		
LL:	-	4.5	10.3	-		
LW:	-	3.5	5.0	-		
<i>Lolium perenne</i>						
FR:	-	1	2	-		
CO:	-	5.0	15.0	-		
HT:	-	2.0	18.5	-		
LL:	-	7.0	19.0	-		
LW:	-	0.2	0.4	-		
<i>Carex spp.</i>						
FR:	-	1	1	-		
CO:	-	20.0	30.0	-		
HT:	-	4.0	17.0	-		
LL:	-	8.0	18.0	-		
LW:	-	0.2	0.5	-		
<i>Thuidium tamarascinum</i>						
FR:	-	1	3	2		
CO:	-	10.0	7.0	15.0		
<i>Urtica dioica</i>						
FR:	-	-	7	7		
CO:	-	-	10.3	15.3	12.5	0.12
HT:	-	-	14.5	22.7	10.0	0.063
LL:	-	-	3.9	5.0	15.5	0.25
LW:	-	-	2.5	3.7	5.5	0.014*
<i>Mercurialis perennis</i>						
FR:	-	-	5	10		
CO:	-	-	15.6	22.5	19.0	0.45
HT:	-	-	15.0	21.7	2.0	0.0047**
LL:	-	-	5.4	5.9	15.5	0.24
LW:	-	-	3.2	2.8	22.5	0.76
<i>Brachythecium rutabulum</i>						
FR:	-	-	1	2		
CO:	-	-	6.0	7.5		
<i>Lonicera periclymenum</i>						
FR:	-	-	10	14		
CO:	-	-	13.5	14.5	68.0	0.90
HT:	-	-	20.3	20.0	62.0	0.64
LL:	-	-	2.8	3.6	40.0	0.077
LW:	-	-	1.9	1.9	64.5	0.75
<i>Quercus robur</i> ^e						
FR:	-	-	2	2		
CO:	-	-	5.0	10.0		
HT:	-	-	14.5	29.0		
LL:	-	-	4.0	4.5		
LW:	-	-	2.2	2.4		
<i>Viola riviniana</i>						
FR:	-	-	6	3		
CO:	-	-	19.5	26.0		
HT:	-	-	8.5	9.4		
LL:	-	-	2.5	2.8		
LW:	-	-	2.6	2.2		
<i>Chamaenerion angustifolium</i>						
FR:	-	-	1	3		
CO:	-	-	25.0	33.3		
HT:	-	-	8.0	32.3		
LL:	-	-	8.5	9.0		
LW:	-	-	2.7	2.1		
<i>Lapsana communis</i>						
FR:	-	-	2	2		

Species	Heavily trampled	Moderately trampled	Lightly trampled	Control untrampled	H or U ^b	p
CO:	-	-	1.2	2.2		
HT:	-	-	14.0	14.5		
LL:	-	-	4.3	6.4		
LW	-	-	3.0	3.8		
<i>Pteridium aquilinum</i>						
FR:	-	-	3	6		
CO:	-	-	8.3	23.3		
HT:	-	-	14.3	26.6		
<i>Deschampsia flexuosa</i>						
FR:	-	-	4	5		
CO:	-	-	22.5	18.0		
HT:	-	-	17.1	12.7		
LL:	-	-	18.7	14.5		
LW	-	-	0.1	0.1		
<i>Ilex aquifolium</i> ^e						
FR:	-	-	1	7		
CO:	-	-	25.0	13.6		
HT:	-	-	40.0	28.1		
LL:	-	-	6.2	5.8		
LW	-	-	3.3	2.6		
<i>Rhytiadelphus triquestris</i>						
FR:	-	-	1	1		
CO:	-	-	15.0	15.0		
<i>Dryopteris dilatata</i>						
FR:	-	-	1	6		
CO:	-	-	35.0	34.2		
HT:	-	-	39.0	46.8		

Species found in only one wear class (m = moderately trampled, l = lightly trampled, c = control)

	Wear class	FR	CO	HT	LL	LW
<i>Galeopsis tetrahit</i>	h	1	6.0	1.2	1.0	0.9
<i>Primula vulgaris</i>	m	1	18.0	8.0	7.0	3.0
<i>Veronica montana</i>	m	1	7.0	3.5	1.1	1.1 ^V
<i>Agrostis</i> spp.	m	1	9.0	3.0	4.0	0.2
<i>Ajuga reptans</i>	m	1	20.0	8.0	3.3	2.0
<i>Cirsium vulgare</i>	m	1	5.0	2.4	4.5	1.9
<i>Veronica chamaedrys</i>	l	1	5.0	2.0	1.0	1.0
<i>Alliaria petiolata</i>	l	2	11.0	8.5	7.0	3.3
<i>Moehringia trinervia</i>	l	1	4.0	16.0	1.2	0.3
<i>Circaea lutetiana</i>	l	2	12.5	6.5	3.0	2.6
<i>Corylus avellana</i> ^e	l	1	6.0	25.0	2.9	1.5
<i>Adoxa moschatellina</i>	l	1	4.0	8.5	1.9	2.4
<i>Fraxinus excelsior</i> ^e	c	1	8.0	29.0	19.0	0.6
<i>Rosa canina</i>	c	1	5.0	20.0	0.9	0.6
<i>Caltha palustris</i>	c	1	14.0	14.0	6.8	5.5
<i>Cirsium arvense</i>	c	1	15.0	32.0	30.0	13.0
<i>Myosotis sylvatica</i>	c	1	20.0	16.0	7.5	2.9
<i>Vicia sepium</i>	c	1	10.0	13.5	2.6	1.4
<i>Lysimachia nummularia</i>	c	3	13.3	6.2	2.9	1.8
<i>Dryopteris filix-mas</i>	c	4	27.5	37.2	-	-
<i>Impatiens glandulifera</i>	c	1	25.0	29.5	12.0	5.3

Total species frequency

18

49

63

61

Mean Shannon's diversity index (H')

0.12

0.29

0.47

0.42

^a - FR = percent frequency (number of quadrats containing the species divided by the total number of quadrats); CO = vegetation cover (%); PH = plant height (cm); LL = leaf length (cm); LW = leaf width (cm) (all expressed as total mean divided by species frequency)

^b - Kruskal-Wallis 'H' statistic for data set comparing 3 or more wear classes; Mann Whitney 'U' statistic for comparing 2 wear classes; *** sig. at p ≤ 0.001; ** sig. at p ≤ 0.01; * sig. at p ≤ 0.05

^c - mix of *Poa annua* and *P. pratensis*

^d - mix of *Holcus mollis* and *H. lanatus*

^e - sapling / seedling

Appendix 2.8 - Mean plant cover (%), frequency (%), height (cm), leaf length (cm) and leaf width (cm)^a in each wear class combined for all three sites in the **summer** survey with the results of statistical tests.

Species		Heavily trampled	Moderately trampled	Lightly trampled	Control untrampled	H or U ^b	p
<i>Poa</i> spp. ^c							
	FR:	26	43	7	-		
	CO:	11.0	17.4	15.0	-	7.1	0.028*
	PH:	1.4	6.2	11.3	-	40.4	<0.001***
	LL:	2.3	6.7	9.5	-	39.4	<0.001***
	LW:	0.2	0.3	0.3	-	19.9	<0.001***
<i>Eurynchium proelongum</i>							
	FR:	5	13	7	1		
	CO:	13.0	19.9	12.7	10.0	3.4	0.33
<i>Deschampsia cespitosa</i>							
	FR:	5	13	19	12		
	CO:	19.8	21.2	31.6	34.8	4.7	0.20
	PH:	3.9	13.3	43.5	45.8	29.9	<0.001***
	LL:	5.3	15.0	32.0	33.3	28.0	<0.001***
	LW:	0.2	0.2	0.4	0.4	26.8	<0.001***
<i>Plantago major</i>							
	FR:	7	11	4	-		
	CO:	6.9	19.4	17.0	-	3.9	0.14
	PH:	1.4	4.8	17.1	-	15.6	<0.001***
	LL:	2.7	5.8	10.9	-	12.8	0.0017**
	LW:	1.6	3.5	7.3	-	12.6	0.0018**
<i>Holcus</i> spp. ^d							
	FR:	4	13	11	3		
	CO:	14.0	20.5	16.9	9.7	3.2	0.36
	PH:	7.2	13.7	21.4	26.0	9.2	0.027*
	LL:	7.4	11.5	14.8	24.2	15.2	0.0017**
	LW:	0.5	0.5	0.7	0.8	15.2	0.13
<i>Dicranum</i> spp.							
	FR:	6	3	1	1		
	CO:	6.8	6.0	10.0	5.0	1.6	0.66
<i>Lolium perenne</i>							
	FR:	2	11	4	-		
	CO:	6.5	16.4	8.7	-	5.5	0.065
	PH:	3.7	8.7	15.5	-	7.2	0.027*
	LL:	6.4	9.0	10.0	-	4.8	0.092
	LW:	0.2	0.4	0.5	-	3.9	0.14
<i>Ranunculus repens</i>							
	FR:	2	6	4	-		
	CO:	6.0	16.3	12.5	-	3.6	0.16
	PH:	0.9	4.3	14.0	-	9.3	0.0096**
	LL:	1.1	2.5	3.3	-	5.5	0.065
	LW:	1.0	2.8	3.6	-	6.2	0.045*
<i>Rubus fruticosus</i> agg.							
	FR:	2	11	52	71		
	CO:	7.5	15.4	24.4	33.4	41.2	<0.001***
	PH:	2.4	10.1	27.7	48.7	50.3	<0.001***
	LL:	1.6	4.6	7.8	8.6	33.8	<0.001***
	LW:	1.3	3.5	5.8	6.3	27.5	<0.001***
<i>Veronica chamaedrys</i>							
	FR:	1	2	5	-		
	CO:	7.0	3.5	10.0	-	4.0	0.13
	PH:	2.0	2.8	10.1	-	5.0	0.082
	LL:	1.7	1.9	3.5	-	5.1	0.079
	LW:	1.0	2.1	3.2	-	3.4	0.18
<i>Mnium hornum</i>							
	FR:	1	5	2	-		
	CO:	16.0	12.2	5.5	-		
<i>Sagina procumbens</i>							
	FR:	1	1	1	-		
	CO:	10.0	15.0	10.0	-		
	PH:	4.5	6.4	10.0	-		
	LL:	0.8	0.9	0.9	-		
	LW:	0.3	0.3	0.4	-		
<i>Taraxacum officinales</i>							
	FR:	1	1	1	-		
	CO:	10.0	10.0	20.0	-		
	PH:	1.2	10.0	11.0	-		
	LL:	13.0	14.5	20.0	-		
	LW:	1.2	1.7	3.7	-		
<i>Stellaria media</i>							
	FR:	2	4	1			
	CO:	2.0	15.0	10.0			
	PH:	2.0	4.5	5.0			
	LL:	0.3	0.5	0.6			
	LW:	0.2	0.3	0.3			
<i>Hedera helix</i>							
	FR:	-	12	20	23		
	CO:	-	9.2	16.1	18.9	2.5	0.28
	PH:	-	4.7	8.0	9.8	23.9	<0.001***
	LL:	-	2.6	4.0	4.5	14.8	<0.001***
	LW:	-	0.3	0.4	0.5	13.7	0.001**
<i>Glechoma hederacea</i>							
	FR:	-	4	4	2		
	CO:	-	12.2	12.7	14.0	0.20	0.91

Species	Heavily trampled	Moderately trampled	Lightly trampled	Control untrampled	H or U ^b	p
PH:	-	3.6	5.7	14.2	7.8	0.020*
LL:	-	2.4	2.5	5.5	4.4	0.11
LW:	-	2.6	2.7	4.5	4.4	0.11
<i>Silene dioica</i>						
FR:	-	4	9	8		
CO:	-	5.0	17.3	24.5	7.1	0.029*
PH:	-	2.6	18.8	25.0	10.0	0.0068**
LL:	-	2.4	7.1	8.4	10.9	0.0043**
LW:	-	1.5	3.5	5.4	11.3	0.0036**
<i>Stellaria holostea</i>						
FR:	-	3	6	3		
CO:	-	11.3	16.5	5.7	1.4	0.49
PH:	-	6.3	14.2	21.3	5.4	0.069
LL:	-	3.6	3.5	4.7	4.0	0.13
LW:	-	0.3	0.3	0.5	4.3	0.11
<i>Oxalis acetosella</i>						
FR:	-	3	9	6		
CO:	-	7.3	11.4	8.8	0.02	0.99
PH:	-	4.0	5.2	7.4	4.1	0.13
LL:	-	1.1	1.6	1.8	4.4	0.11
LW:	-	1.3	1.8	2.3	5.4	0.066
<i>Geum urbanum</i>						
FR:	-	7	6	-		
CO:	-	25.7	24.2	-	24.5	0.61
PH:	-	10.0	30.2	-	1.0	0.004**
LL:	-	3.4	7.0	-	0.0	0.0027**
LW:	-	4.0	7.6	-	0.0	0.0027**
<i>Lapsana communis</i>						
FR:	-	3	4	1		
CO:	-	12.3	18.7	25.0	4.0	0.13
PH:	-	10.0	22.5	19.0	5.9	0.052
LL:	-	5.5	3.9	5.5	5.1	0.078
LW:	-	3.4	3.7	3.4	0.1	0.95
<i>Brachypodium sylvaticum</i>						
FR:	-	3	7	-		
CO:	-	5.3	12.1	-	3.0	0.084
PH:	-	1.4	2.8	-	2.5	0.067
LL:	-	6.1	16.7	-	0.0	0.015*
LW:	-	5.2	11.0	-	0.0	0.015*
<i>Pteridium aquilinum</i>						
FR:	-	3	16	35		
CO:	-	17.7	32.7	39.5	3.7	0.15
PH:	-	36.7	78.0	95.7	5.3	0.069
<i>Acer pseudoplatanus</i> ^e						
FR:	-	4	3	2		
CO:	-	5.0	4.0	9.5		
PH:	-	6.5	6.6	7.7		
LL:	-	4.0	3.0	3.6		
LW:	-	2.1	1.7	1.8		
<i>Dactylis glomerata</i>						
FR:	-	2	11	1		
CO:	-	9.0	20.2	15.0	2.9	0.24
PH:	-	2.7	26.2	29.0	4.9	0.084
LL:	-	7.7	18.4	30.0	6.4	0.041*
LW:	-	0.4	0.6	1.0	5.6	0.062
<i>Rumex obtusifolius</i>						
FR:	-	4	5	1		
CO:	-	7.5	21.2	21.0	4.7	0.096
PH:	-	6.7	21.8	40.0	6.9	0.032*
LL:	-	5.4	12.2	10.0	7.0	0.030*
LW:	-	3.5	6.3	2.5	3.2	0.20
<i>Ranunculus acris</i>						
FR:	-	1	3	6		
CO:	-	25.0	28.5	13.5		
PH:	-	6.5	17.3	16.2		
LL:	-	2.5	6.6	6.5		
LW:	-	2.6	4.8	4.3		
<i>Bromus ramosus</i>						
FR:	-	1	12	10		
CO:	-	10.0	18.7	26.0	1.8	0.41
PH:	-	26.0	18.3	26.2	6.8	0.034*
LL:	-	9.0	19.1	21.1	3.1	0.21
LW:	-	1.0	1.0	2.8	6.4	0.041*
<i>Juncus spp.</i>						
FR:	-	1	5	1		
CO:	-	15.0	34.0	70.0		
PH:	-	1.5	36.4	31.0		
LL:	-	1.6	48.8	60.0		
LW:	-	0.2	0.3	0.3		
<i>Anthoxanthum odoratum</i>						
FR:	-	4	5	2		
CO:	-	22.5	26.0	10.0		
PH:	-	17.2	29.2	30.0		
LL:	-	8.1	11.0	9.5		
LW:	-	0.5	0.5	0.5		
<i>Digitalis purpurea</i>						
FR:	-	2	5	3		
CO:	-	12.5	38.0	26.7	6.6	0.037*
PH:	-	7.0	24.0	31.7	5.3	0.067
LL:	-	8.8	20.6	21.3	4.4	0.11
LW:	-	6.0	13.6	11.3	4.9	0.087
<i>Rumex sanguineus</i>						
FR:	-	1	2	-		
CO:	-	21.0	15.0	-		
PH:	-	3.4	31.0	-		
LL:	-	6.0	9.4	-		

Species	Heavily trampled	Moderately trampled	Lightly trampled	Control untrampled	H or U ^b	p
<i>Lysimachia nemorum</i>	-	3.7	3.0	-		
FR:	-	1	3	-		
CO:	-	5.0	41.7	-		
PH:	-	4.0	9.5	-		
LL:	-	1.5	2.5	-		
LW:	-	1.3	2.1	-		
<i>Agrostis</i> spp.	-	-	-	-		
FR:	-	3	1	-		
CO:	-	25.0	15.0	-		
PH:	-	17.5	16.0	-		
LL:	-	6.7	6.0	-		
LW:	-	0.3	0.3	-		
<i>Lysimachia nummularia</i>	-	-	-	-		
FR:	-	1	3	-		
CO:	-	10.0	20.0	-		
PH:	-	10.0	14.0	-		
LL:	-	1.4	1.8	-		
LW:	-	1.3	1.7	-		
<i>Prunella vulgaris</i>	-	-	-	-		
FR:	-	1	2	-		
CO:	-	40.0	25.0	-		
PH:	-	9.0	40.0	-		
LL:	-	2.0	6.5	-		
LW:	-	1.0	3.0	-		
<i>Rhyniadelphus triquestris</i>	-	-	-	-		
FR:	-	1	1	-		
CO:	-	5.0	5.0	-		
<i>Plagiomnium undulatum</i>	-	-	-	-		
FR:	-	1	1	-		
CO:	-	30.0	40.0	-		
<i>Carex</i> spp.	-	-	-	-		
FR:	-	1	-	2		
CO:	-	30.0	-	20.0		
PH:	-	20.0	-	29.0		
LL:	-	20.0	-	21.0		
LW:	-	0.6	-	0.8		
<i>Crataegus monogyna</i> ^e	-	-	-	-		
FR:	-	1	-	1		
CO:	-	4.0	-	9.0		
PH:	-	4.8	-	38.0		
LL:	-	2.2	-	4.0		
LW:	-	1.4	-	2.2		
<i>Pseudoscleropodium purum</i>	-	-	-	-		
FR:	-	1	-	1		
CO:	-	10.0	-	30.0		
<i>Alliaria petiolata</i>	-	-	-	-		
FR:	-	1	1	2		
CO:	-	4.0	16.0	15.0		
PH:	-	2.0	22.0	51.0		
LL:	-	2.5	5.5	8.8		
LW:	-	1.8	6.5	9.4		
<i>Polytrichum</i> spp.	-	-	-	-		
FR:	-	1	2	2		
CO:	-	15.0	12.5	7.5		
<i>Leucobryum glaucum</i>	-	-	-	-		
FR:	-	1	1	1		
CO:	-	5.0	20.0	5.0		
<i>Mercurialis perennis</i>	-	-	-	-		
FR:	-	-	2	9		
CO:	-	-	25.0	32.7	7.0	0.64
PH:	-	-	25.0	30.9	0.0	0.033*
LL:	-	-	8.2	9.0	8.5	0.90
LW:	-	-	3.6	3.9	6.5	0.55
<i>Galium aparine</i>	-	-	-	-		
FR:	-	-	4	6		
CO:	-	-	5.0	10.0	5.0	0.13
PH:	-	-	26.0	22.3	19.0	0.13
LL:	-	-	1.4	1.3	15.5	0.44
LW:	-	-	0.4	0.3	16.0	0.33
<i>Hyacinthoides non-scripta</i>	-	-	-	-		
FR:	-	-	8	8		
CO:	-	-	2.4	3.7	14.5	0.057
PH:	-	-	36.9	36.7	34.0	0.83
<i>Urtica dioica</i>	-	-	-	-		
FR:	-	-	5	12		
CO:	-	-	15.6	18.4	28.5	0.87
PH:	-	-	32.7	44.6	12.5	0.063
LL:	-	-	8.3	8.6	27.0	0.75
LW:	-	-	3.9	5.8	18.5	0.22
<i>Dryopteris filix-mas</i>	-	-	-	-		
FR:	-	-	2	8		
CO:	-	-	27.5	33.1	15.0	0.42
PH:	-	-	54.5	48.4	9.5	0.69
<i>Ilex aquifolium</i> ^e	-	-	-	-		
FR:	-	-	9	6		
CO:	-	-	18.1	26.7	12.0	0.07
PH:	-	-	28.0	58.0	15.5	0.17
LL:	-	-	7.6	8.9	14.0	0.12
LW:	-	-	2.6	2.8	28.0	0.90
<i>Chamaenerion angustifolium</i>	-	-	-	-		
FR:	-	-	3	7		
CO:	-	-	28.3	35.0	5.0	0.19
PH:	-	-	73.0	111.4	6.5	0.36
LL:	-	-	10.3	10.6	10.0	0.90
LW:	-	-	2.7	2.1	17.0	0.11

<i>Circaea lutetiana</i>			6	3		
FR:	-	-	18.3	20.3		
CO:	-	-	19.1	25.0		
PH:	-	-	5.6	6.0		
LL:	-	-	3.3	3.8		
LW	-	-				
<i>Lonicera periclymenum</i>			10	11		
FR:	-	-	21.9	16.4	0.6	0.64
CO:	-	-	24.3	24.7	0.5	0.92
PH:	-	-	4.0	3.8	74.0	0.16
LL:	-	-	2.2	2.3	48.5	0.64
LW	-	-				
<i>Dryopteris diluata</i>			2	4		
FR:	-	-	20.0	30.0	3.0	0.63
CO:	-	-	45.5	40.5	5.0	0.64
PH:	-	-				
<i>Deschampsia flexuosa</i>			2	6		
FR:	-	-	37.5	18.3		
CO:	-	-	14.0	15.7		
PH:	-	-	19.0	17.0		
LL:	-	-	1.5	1.5		
LW	-	-				
<i>Dryopteris affinis</i>			1	5		
FR:	-	-	20.0	32.0		
CO:	-	-	30.0	43.6		
PH:	-	-				
<i>Thuidium tamarascinum</i>			3	3		
FR:	-	-	10.0	11.7		
CO:	-	-				
<i>Arctium minus</i>			1	2		
FR:	-	-	10.0	54.0		
CO:	-	-	23.5	80.0		
PH:	-	-	35.0	28.0		
LL:	-	-	17.0	18.0		
LW	-	-				
<i>Epilobium montanum</i>			1	2		
FR:	-	-	8.0	13.0		
CO:	-	-	30.0	40.0		
PH:	-	-	9.5	9.8		
LL:	-	-	1.8	2.4		
LW	-	-				
<i>Heracleum sphondylium</i>			1	1		
FR:	-	-	40.0	64.0		
CO:	-	-	100.0	170.0		
PH:	-	-	16.0	17.0		
LL:	-	-	14.5	17.5		
LW	-	-				
<i>Corylus avellana</i> *			1	1		
FR:	-	-	35.0	40.0		
CO:	-	-	49.0	49.0		
PH:	-	-	12.0	13.0		
LL:	-	-	10.5	11.0		
LW	-	-				
<i>Populus tremula</i> *			1	1		
FR:	-	-	9.8	8.0		
CO:	-	-	30.0	55.0		
PH:	-	-	10.0	12.0		
LL:	-	-	7.0	7.5		
LW	-	-				
<i>Impatiens glandulifera</i>			1	2		
FR:	-	-	15.0	25.0		
CO:	-	-	37.0	100.0		
PH:	-	-	11.0	9.0		
LL:	-	-	5.0	3.5		
LW	-	-				
<i>Galeopsis tetrahit</i>			3	2		
FR:	-	-	56.7	17.5		
CO:	-	-	57.0	60.0		
PH:	-	-	10.0	10.5		
LL:	-	-	4.5	4.0		
LW	-	-				
<i>Sorbus aucuparia</i> *			1	4		
FR:	-	-	10.0	27.5		
CO:	-	-	29.0	70.0		
PH:	-	-	2.0	2.4		
LL:	-	-	1.2	1.6		
LW	-	-				
<i>Hylocomium splendens</i>			1	1		
FR:	-	-	10.0	25.0		
CO:	-	-				
<i>Cirsium vulgare</i>			1	1		
FR:	-	-	40.0	20.0		
CO:	-	-	120.0	60.0		
PH:	-	-	22.0	18.0		
LL:	-	-	6.5	4.0		
LW	-	-				
<i>Brachythecium purum</i>			2	2		
FR:	-	-	10.0	12.5		
CO:	-	-				
<i>Teucrium scorodonia</i>			1	1		
FR:	-	-	25.0	80.0		
CO:	-	-	40.0	50.0		
PH:	-	-	8.0	8.0		
LL:	-	-	4.2	4.2		
LW	-	-				
<i>Rubus idaeus</i>			1	1		
FR:	-	-	25.0	30.0		
CO:	-	-				

PH:	-	-	100.0	155.0
LL:	-	-	11.0	10.5
LW:	-	-	6.7	8.0
<i>Galium saxatile</i>				
FR:	-	-	1	2
CO:	-	-	10.0	7.5
PH:	-	-	10.0	18.0
LL:	-	-	0.3	0.3
LW:	-	-	0.2	0.2

Species found in only one wear class (m = moderately trampled, l = lightly trampled, c = control)

	Wear class	FR	CO	HT	LL	LW
<i>Fragaria vesca</i>	m	1	10.0	10.0	2.5	2.8
<i>Trifolium repens</i>	m	1	10.0	6.0	1.5	2.5
<i>Viola riviniana</i>	l	4	21.7	9.5	4.0	3.2
<i>Galeobdolon luteum</i>	l	1	36.0	39.0	9.0	4.2A
<i>Anemone nemorosa</i>	l	2	5.5	3.0	4.0	1.4
<i>Hypnum cupressiforme</i>	l	1	5.0	-	-	-
<i>Moehringia trinervia</i>	l	1	14.0	12.0	1.2	0.4
<i>Festuca gigantea</i>	l	1	10.0	34.0	12.0	0.3
<i>Pohlia nutans</i>	l	1	12.0	-	-	-
<i>Malva sylvestris</i>	l	2	10.0	22.0	8.0	7.2
<i>Prunus avium</i> ^e	l	1	35.0	50.0	7.0	5.7
<i>Mnium affine</i>	l	1	40.0	-	-	-
<i>Arrhenatherum elatius</i>	l	1	10.0	25.0	21.0	0.7
<i>Epilobium hirsutum</i>	l	1	10.0	30.0	5.0	2.1
<i>Epilobium spp</i>	l	1	20.0	34.0	7.0	3.7
<i>Stachys sylvatica</i>	c	1	12.0	30.4	5.2	3.1
<i>Milium effusum</i>	c	2	8.0	54.0	12.5	0.7
<i>Plagiominium undulatum</i>	c	2	4.5	-	-	-
<i>Dicranella heteromalla</i>	c	2	7.0	-	-	-
<i>Acer campestre</i> ^e	c	1	11.0	50.0	9.0	10.0
<i>Rosa canina</i>	c	2	14.5	40.0	3.4	1.7
<i>Angelica sylvestris</i>	c	2	27.0	70.0	8.0	3.7
<i>Aegopodium podagraria</i>	c	2	13.0	110.0	9.5	4.1
<i>Brachythecium rutabulum</i>	c	3	12.0	-	-	-
<i>Solanum dulcamara</i>	c	1	20.0	66.0	9.9	2.4
<i>Quercus robur</i> ^e	c	3	29.7	37.5	6.5	3.5
<i>Arum maculatum</i>	c	1	4.0	29.0	-	-
<i>Phragmites australis</i>	c	1	7.0	30.4	32.0	1.1
<i>Veronica montana</i>	c	2	8.0	3.9	1.9	1.8
<i>Myosotis sylvatica</i>	c	1	20.0	17.0	7.7	3.0
<i>Hieracium spp.</i>	c	1	40.0	50.0	10.8	4.0
<i>Castanea sativa</i> ^e	c	1	20.0	39.0	12.0	7.0

Total species frequency

13

45

81

71

Mean Shannon's diversity index (*H'*)

0.14

0.29

0.46

0.41

^a - FR = percent frequency (number of quadrats containing the species divided by the total number of quadrats); CO = vegetation cover (%); PH = plant height (cm); LL = leaf length (cm); LW = leaf width (cm) (all expressed as total mean divided by species frequency)

^b - Kruskal-Wallis 'H' statistic for data set comparing 3 or more wear classes; Mann Whitney 'U' statistic for comparing 2 wear classes; *** sig. at $p \leq 0.001$; ** sig. at $p \leq 0.01$; * sig. at $p \leq 0.05$

^c - mix of *Poa annua* and *P. pratensis*

^d - mix of *Holcus mollis* and *H. lanatus*

^e - sapling / seedling

Appendix 2.9 - Mean plant cover (%), frequency (%), height (cm), leaf length (cm) and leaf width (cm)^a in each wear class combined for all three sites in the **autumn** survey with the results of statistical tests.

Species		Heavily trampled	Moderately trampled	Lightly trampled	Control untrampled	H or U ^b	p
<i>Poa</i> spp. ^c							
	FR:	15	33	7	-		
	CO:	7.5	13.5	6.0	-	7.1	0.020*
	PH:	1.3	4.6	8.9	-	26.7	<0.001***
	LL:	2.7	5.8	9.0	-	23.7	<0.001***
	LW:	0.2	0.2	0.3	-	3.8	0.15
<i>Rubus fruticosus</i> agg.							
	FR:	4	24	56	69		
	CO:	6.7	9.3	27.1	32.2	57.0	<0.001***
	PH:	6.1	6.5	25.0	37.8	75.4	<0.001***
	LL:	4.0	4.3	5.8	6.6	32.4	<0.001***
	LW:	2.2	3.1	4.1	4.7	28.6	<0.001***
<i>Eurynchium praelongum</i>							
	FR:	4		7	3		
	CO:	9.7	9	11.4	5.0	1.2	0.74
<i>Taraxacum officinales</i>							
	FR:	1	4	3	-		
	CO:	12.0	12.0	18.7	-		
	PH:	3.5	4.5	9.5	-		
	LL:	8.0	4.8	12.3	-		
	LW:	1.8	1.9	4.4	-		
<i>Deschampsia cespitosa</i>							
	FR:	2	19	15	8		
	CO:	15.0	18.2	28.0	32.5	7.2	0.063
	PH:	4.9	9.6	24.2	25.7	21.5	<0.001***
	LL:	9.4	11.9	26.4	30.4	19.1	<0.001***
	LW:	0.2	0.2	0.3	0.3	13.5	0.0036**
<i>Ranunculus acris</i>							
	FR:	1	5	2	-		
	CO:	4.0	8.4	12.5	-		
	PH:	2.0	4.2	12.5	-		
	LL:	0.6	1.8	4.0	-		
	LW:	0.5	2.3	4.1	-		
<i>R. repens</i>							
	FR:	1	2	-	-		
	CO:	4.0	5.0	-	-		
	PH:	2.0	6.0	-	-		
	LL:	1.4	2.1	-	-		
	LW:	1.5	1.7	-	-		
<i>Dicranum</i> spp.							
	FR:	2	1	-	-		
	CO:	4.5	5.0	-	-		
<i>Juncus</i> spp.							
	FR:	1	2	5	1		
	CO:	5.0	21.0	22.0	15.0		
	PH:	1.2	14.5	37.5	62.0		
	LL:	6.5	22.0	50.0	63.0		
	LW:	0.1	0.3	0.4	0.2		
<i>Pleurozium schreberi</i>							
	FR:	1	2	4	2		
	CO:	5.0	12.5	21.0	20.0		
<i>Digitalis purpurea</i>							
	FR:	1	3	4	5		
	CO:	6.0	31.7	26.2	24.0		
	PH:	3.5	10.7	15.7	19.2		
	LL:	2.5	7.0	13.5	16.0		
	LW:	2.0	4.5	8.3	9.1		
<i>Hederu helix</i>							
	FR:	-	11	19	18		
	CO:	-	5.8	11.4	10.4	5.5	0.064
	PH:	-	5.0	6.2	7.7	7.8	0.020*
	LL:	-	2.5	3.5	3.9	9.2	0.0098**
	LW:	-	2.8	3.5	4.3	8.2	0.016*
<i>Glechoma hederacea</i>							
	FR:	-	2	2	2		
	CO:	-	3.0	13.5	23.0		
	PH:	-	1.6	5.3	8.5		
	LL:	-	0.8	1.9	3.2		
	LW:	-	1.3	2.2	2.9		
<i>Silene dioica</i>							
	FR:	-	2	5	5		
	CO:	-	7.5	14.6	20.4		
	PH:	-	3.5	8.3	8.3		
	LL:	-	3.6	5.6	5.9		
	LW:	-	1.5	3.3	3.2		
<i>Geum urbanum</i>							
	FR:	-	3	3	2		
	CO:	-	5.7	16.7	18.0		
	PH:	-	4.8	9.3	7.0		
	LL:	-	1.7	4.2	6.0		
	LW:	-	2.3	6.2	5.0		
<i>Holcus</i> spp. ^d							
	FR:	-	14	14	8		
	CO:	-	10.3	14.7	9.5	0.1	0.95

Species	Heavily trampled	Moderately trampled	Lightly trampled	Control untrampled	H or U ^b	p
	PH: -	6.8	12.9	11.5	8.9	0.014*
	LL: -	7.9	12.6	11.8	4.7	0.094
	LW: -	0.3	0.4	0.4	1.8	0.414
<i>Veronica chamaedrys</i>	FR: -	3	3	1		
	CO: -	11.3	8.7	12.0		
	PH: -	3.8	6.2	7.4		
	LL: -	2.2	2.8	2.5		
	LW: -	2.0	1.7	2.8		
<i>Dracopis dilatata</i>	FR: -	1	6	8		
	CO: -	10.0	22.5	35.6		
	PH: -	16.0	47.8	34.5		
<i>Urtica dioica</i>	FR: -	2	9	5		
	CO: -	5.5	19.7	14.2	3.6	0.16
	PH: -	4.5	19.5	39.1	6.5	0.039*
	LL: -	1.7	4.6	4.6	4.7	0.094
	LW: -	1.5	3.7	3.7	4.6	0.098
<i>Brachypodium sylvaticum</i>	FR: -	2	4	1		
	CO: -	5.5	8.2	15.0		
	PH: -	8.9	26.0	21.5		
	LL: -	6.5	17.7	20.0		
	LW: -	0.4	0.8	0.9		
<i>Oxalis acetosella</i>	FR: -	1	7	6		
	CO: -	8.0	10.7	9.3		
	PH: -	4.0	6.9	5.4		
	LL: -	1.4	1.3	0.9		
	LW: -	1.0	1.2	1.1		
<i>Viola riviniana</i>	FR: -	1	2	1		
	CO: -	5.0	11.0	15.0		
	PH: -	6.0	7.7	12.0		
	LL: -	2.2	3.0	3.3		
	LW: -	2.2	2.7	3.4		
<i>Lonicera periclymenum</i>	FR: -	1	8	12		
	CO: -	6.0	4.9	7.9	4.3	0.12
	PH: -	6.5	30.5	40.0	3.9	0.14
	LL: -	1.0	1.7	2.8	10.7	0.0046**
	LW: -	0.4	1.0	1.4	6.7	0.036*
<i>Brachythecium purum</i>	FR: -	1	1	1		
	CO: -	5.0	15.0	5.0		
<i>Thuidium tamariscinum</i>	FR: -	2	5	3		
	CO: -	6.0	6.7	7.7		
<i>Polytrichum spp.</i>	FR: -	1	3	2		
	CO: -	10.0	21.7	8.5		
<i>Alliaria petiolata</i>	FR: -	2	-	1		
	CO: -	7.5	-	18.0		
	PH: -	5.9	-	14.4		
	LL: -	3.4	-	4.1		
	LW: -	3.6	-	5.0		
<i>Hypnum cupressiforme</i>	FR: -	2	-	1		
	CO: -	11.0	-	4.0		
<i>Mnium hornum</i>	FR: -	3	3	2		
	CO: -	12.0	4.3	9.0		
<i>Acer pseudoplatanus</i> ^e	FR: -	1	1	1		
	CO: -	5.0	6.0	5.0		
	PH: -	8.1	13.0	9.0		
	LL: -	5.0	4.0	6.0		
	LW: -	3.2	3.3	4.1		
<i>Plantago major</i>	FR: -	2	2	-		
	CO: -	6.5	17.5	-		
	PH: -	3.2	11.0	-		
	LL: -	3.1	8.7	-		
	LW: -	2.1	4.5	-		
<i>Carex spp.</i>	FR: -	1	2	-		
	CO: -	25.0	12.5	-		
	PH: -	6.5	18.0	-		
	LL: -	12.0	19.0	-		
	LW: -	0.6	0.8	-		
<i>Stellaria media</i>	FR: -	6	4	-		
	CO: -	7.3	4.5	-		
	PH: -	4.0	6.1	-		
	LL: -	0.6	0.5	-		
	LW: -	0.4	0.4	-		
<i>Lysimachia nummularia</i>	FR: -	1	2	-		
	CO: -	15.0	9.5	-		
	PH: -	2.5	4.2	-		
	LL: -	3.0	3.1	-		
	LW: -	2.0	2.1	-		
<i>Leucobryum glaucum</i>	FR: -	1	1	-		

Species	Heavily trampled	Moderately trampled	Lightly trampled	Control untrampled	H or U ^b	p
<i>Rumex obtusifolius</i>	-	4.0	12.0	-		
FR:	-	3	3	-		
CO:	-	6.7	12.0	-		
PH:	-	3.1	6.6	-		
LL:	-	6.2	8.2	-		
LW:	-	2.6	5.1	-		
<i>Stellario holostea</i>	-	-	4	3		
FR:	-	-	9.7	4.3		
CO:	-	-	11.5	12.7		
PH:	-	-	3.0	2.8		
LL:	-	-	0.3	0.2		
LW:	-	-	3	7		
<i>Mercurialis perennis</i>	-	-	18.0	18.6		
FR:	-	-	23.2	21.0		
CO:	-	-	6.3	6.7		
PH:	-	-	3.1	3.1		
LL:	-	-	1	1		
LW:	-	-	20.0	60.0		
<i>Dryopteris affinis</i>	-	-	40.0	120.0		
FR:	-	-	6	16		
CO:	-	-	29.7	36.0		
PH:	-	-	51.0	74.4		
<i>Pteridium aquilinum</i>	-	-	5	2		
FR:	-	-	13.4	13.0		
CO:	-	-	12.1	13.4		
PH:	-	-	1.4	1.7		
LL:	-	-	1.0	1.0		
LW:	-	-	5	3		
<i>Galium aparine</i>	-	-	9.8	8.0		
FR:	-	-	7.8	8.0		
CO:	-	-	0.8	0.5		
PH:	-	-	0.4	0.4		
LL:	-	-	2	2		
LW:	-	-	11.5	22.0		
<i>Brachythecium rutabulum</i>	-	-	1	1		
FR:	-	-	10	8		
CO:	-	-	17.4	13.2		
PH:	-	-	27.3	30.4		
LL:	-	-	7.1	7.3		
LW:	-	-	3.0	3.7		
<i>Hylocomium splendens</i>	-	-	5	3		
FR:	-	-	20.0	18.3		
CO:	-	-	20.6	20.0		
PH:	-	-	15.4	26.3		
LL:	-	-	1.0	1.1		
LW:	-	-	3	6		
<i>Ilex aquifolium</i> ^e	-	-	21.7	19.2		
FR:	-	-	9.3	28.0		
CO:	-	-	15.0	35.2		
PH:	-	-	0.1	0.2		
LL:	-	-	1	1		
LW:	-	-	10.0	10.0		
<i>Bromus ramosus</i>	-	-	10	8		
FR:	-	-	17.4	13.2		
CO:	-	-	27.3	30.4		
PH:	-	-	7.1	7.3		
LL:	-	-	3.0	3.7		
LW:	-	-	5	3		
<i>Deschampsia flexuosa</i>	-	-	20.0	18.3		
FR:	-	-	20.6	20.0		
CO:	-	-	15.4	26.3		
PH:	-	-	1.0	1.1		
LL:	-	-	3	6		
LW:	-	-	21.7	19.2		
<i>Chamaenerion angustifolium</i>	-	-	9.3	28.0		
FR:	-	-	15.0	35.2		
CO:	-	-	0.1	0.2		
PH:	-	-	1	1		
LL:	-	-	10.0	10.0		
LW:	-	-	12.0	70.0		
<i>Sorbus aucuparia</i> ^e	-	-	7.5	9.5		
FR:	-	-	1.4	2.0		
CO:	-	-	1	1		
PH:	-	-	5.0	15.0		
LL:	-	-	6.0	40.0		
LW:	-	-	1.0	3.5		
<i>Plantaginium undulatum</i>	-	-	0.4	1.9		
FR:	-	-	1	3		
CO:	-	-	40.0	5.0		

Species found in only one wear class (m = moderately trampled, l = lightly trampled, c = control)

	Wear class	FR	CO	HT	LL	LW
<i>Arctium minus</i>	l	1	18.0	10.8	12.0	10.0
<i>Veronica montana</i>	l	1	10.0	12.0	1.2	1.0
<i>Vicia sepium</i>	l	1	9.0	4.2	-	-
<i>Dactylis glomerata</i>	l	4	22.2	19.3	14.8	0.3
<i>Lapsana communis</i>	l	1	5.0	7.0	0.7	0.8
<i>Cardamine pratensis</i>	l	1	20.0	7.0	1.2	1.6
<i>Rubus idaeus</i>	l	1	20.0	15.0	5.0	3.2
<i>Stachys sylvatica</i>	l	1	10.0	10.0	3.0	2.4
<i>Epilobium montanum</i>	l	1	15.0	28.0	5.0	2.5
<i>Quercus robur</i> ^e	c	3	13.0	45.5	6.9	4.6
<i>Rosa canina</i>	c	1	20.0	30.0	3.4	1.9
<i>Filipendula ulmaria</i>	c	2	20.0	24.0	8.4	12.0

	Wear class	FR	CO	HT	LL	LW
<i>Impatiens glandulifera</i>	c	2	17.0	35.5	9.7	6.2
<i>Prunella vulgaris</i>	c	1	10.0	16.0	7.0	4.4
<i>Cirsium vulgare</i>	c	1	10.0	5.0	27.0	11.0
<i>Corylus avellana</i> ^e	c	2	25.0	24.0	9.7	6.7
Total species frequency			11	37	57	48

^a - FR = percent frequency (number of quadrats containing the species divided by the total number of quadrats); CO = vegetation cover (%); PH = plant height (cm); LL = leaf length (cm); LW = leaf width (cm) (all expressed as total mean divided by species frequency)

^b - Kruskal-Wallis 'H' statistic for data set comparing 3 or more wear classes; Mann Whitney 'U' statistic for comparing 2 wear classes; *** sig. at p ≤ 0.001; ** sig. at p ≤ 0.01; * sig. at p ≤ 0.05

^c - mix of *Poa annua* and *P. pratensis*

^d - mix of *Holcus mollis* and *H. lanatus*

^e - sapling / seedling

Appendix 3.1

Descriptions of vegetation sub-community types

- *Hyacinthoides non-scripta* dominated sub-community

The European endemic *Hyacinthoides non-scripta* (bluebell) is a monocotyledonous rosette forming geophyte that can be locally dominant in the field layer of deciduous woodland (Grime *et al.* 1990⁸⁸). It is perceived by the public to be Britain's most characteristic English woodland wildflower (Packham & Cohn 1990), and the striking swathes of bluebells carpeting the countryside have heralded the advent of spring down the ages. More abundant in broadleaf than coniferous woodlands and unable to persist in grassland (Blackman & Rutter 1950), the phenology is characteristic of the vernal aspect of deciduous woodland. Thus, the bulk of seasonal above ground growth is complete before the overstory leaf canopy fully develops.

With increasing shade, there is a reduction in the number and size of leaves and overall reproductive potential (Blackman & Rutter 1954, Grabham & Packham 1983, Knight 1964, Rodwell 1991, Thompson & Cox 1978), and it is not found where the mean light intensity between April and mid-June falls below 0.1 of full daylight (Blackman & Rutter 1954). The species regenerates mainly by seed (Wilson 1959, Knight 1964, Grabham & Packham 1983) and vegetative regeneration appears to be of minor importance (Grime *et al.* 1988). The first leaves appear in winter, having developed from initials laid down in the previous year, and spear upwards through deep layers of leaf litter (Grime *et al.* 1988). With further growth arrested into mid-March, leaves are then fully extended and inflorescences unfold from the erect flowering scapes in late spring (Blackman & Rutter 1954). In early summer, flowering comes to an end and seed capsules form, vegetation biomass senesces and seeds are discharged in late summer (Grabham & Packham 1983).

Although *Hyacinthoides non-scripta* is extremely abundant in deciduous woodlands in the British Isles, in some lowland areas it is reported to be largely confined to ancient 'bluebell' woodlands and may therefore be declining (Grime *et al.* 1988, Rodwell 1991, Thompson & Cox 1978). It is known to be susceptible to trampling, grazing and mowing (Blackman & Rutter 1954, Peace & Gilmour 1949).

- *Pteridium aquilinum* dominated sub-community

Although originally a woodland species and a legacy of the once widespread oak woodlands (Tansley 1953, Watt 1976), *Pteridium aquilinum* (bracken) forms a significant component of acid broadleaf woodland and scrub and is a successful weed species (Biggin 1982). It is an invasive fern ally that is capable of vigorous spread into open hill pastures, woodland and wasteland (Grime *et al.* 1988).

A perennial geophyte, fronds emerge in late spring from deep, underground rhizomes and persist until autumn (Page 1982). Established stands regenerate vegetatively to induce dense clonal patches which shade and smother subordinate species. In the open W10 community, *Pteridium aquilinum* forms an impenetrable jungle of vegetation up to 2 m high. Growth tends to be suppressed under impoverished light climates to give sparser, shorter and less vigorous fronds (Biggin 1982, Rodwell 1991). Remaining common in Britain, it is a uniquely competitive and invasive species in many lowland areas (Grime *et al.* 1988), and although young shoots are vulnerable to frost and trampling damage it is not easy to eradicate once established (Grime *et al.* 1988, McCreath 1982).

- *Rubus fruticosus* agg. dominated sub-community

Most characteristic of woodland, scrub and hedgerow habitats, the woody perennial *Rubus fruticosus* agg. (bramble) is capable of local dominance of herbaceous vegetation with its arching, spiny and erect stems (Grime *et al.* 1988). It regenerates mainly vegetatively, and possesses leaves that overwinter and are replaced by new growth early in the growing season. *Rubus fruticosus* agg. grows most vigorously under open canopies, with summer leaves unfolding on new lateral shoots and often forming self shading foliage (Rodwell 1991). Bramble flowers from June to September with seeds produced from September, although heavy shade suppresses reproductive potential (Grime *et al.* 1988).

It is capable of strangling subordinate vegetation by inducing impenetrable underscrub, and in the W10 community is often associated with *Lonicera*

periclymenum. The species is encouraged by the increased disturbance associated with modern forestry management (Grime *et al.* 1988).

Appendix 5.1 - Surface soil (0 - 10 cm depth) bulk density (g cm⁻³), particle density (g cm⁻³), total porosity (%), water filled porosity / volumetric water content (cm³ water filled pores cm⁻³ soil), air filled porosity (cm³ air filled pores cm⁻³ soil), gravimetric water content (g H₂O g⁻¹ soil), organic matter content (%) and pH in the four wear classes of each site and as a site mean with the results of the ranked ANOVA and Tukey tests.

Site	H Heavy	M Moderate	L Light	C Control	df	F test ^a	Tukey HSD
<i>Overall</i>							
Bulk density	1.388 ± 0.025	1.325 ± 0.019	1.069 ± 0.0118	0.892 ± 0.019	311	290.4*** ^c	(H>M>L>C) ^d
Particle density	2.332 ± 0.010	2.344 ± 0.008	2.344 ± 0.008	2.354 ± 0.008	311	2.0	(H=M=L=C)
Total porosity	40.34 ± 1.191	43.22 ± 0.823	54.34 ± 0.844	62.13 ± 0.791	311	71.4***	C>L>M>H
Water filled porosity	0.345 ± 0.014	0.341 ± 0.011	0.360 ± 0.014	0.397 ± 0.018	103	3.1*	(C>M)=L=H
Air filled porosity	0.059 ± 0.009	0.093 ± 0.008	0.184 ± 0.011	0.222 ± 0.016	103	43.8***	C=L>(M=H)
Gravimetric water content	0.254 ± 0.014	0.261 ± 0.012	0.342 ± 0.018	0.455 ± 0.028	103	24.3***	(C>L)>(M=H)
Organic matter content	23.09 ± 1.701	24.48 ± 1.639	32.33 ± 2.256	43.93 ± 2.764	103	19.9***	(C>L)>(M=H)
pH	4.863 ± 0.055	4.758 ± 0.066	4.375 ± 0.053	4.184 ± 0.046	103	33.3***	(H=M)>(L=C)
<i>Tocil Wood</i>							
Bulk density	1.364 ± 0.037	1.296 ± 0.032	1.033 ± 0.028	0.835 ± 0.024	155	138.0***	(H=M)>(L>C)
Particle density	2.303 ± 0.014	2.343 ± 0.013	2.341 ± 0.013	2.350 ± 0.013	155	5.0*	(C=L=M)>H
Total porosity	40.67 ± 1.881	44.18 ± 1.350	55.80 ± 1.324	64.44 ± 1.105	155	127.2***	(C>L)>M>H
Water filled porosity	0.351 ± 0.025	0.345 ± 0.021	0.353 ± 0.020	0.402 ± 0.028	51	1.2	(C=L=M=H)
Air filled porosity	0.058 ± 0.014	0.101 ± 0.014	0.205 ± 0.015	0.243 ± 0.022	51	26.9***	(C=L)>(M=H)
Gravimetric water content	0.265 ± 0.026	0.271 ± 0.022	0.349 ± 0.029	0.498 ± 0.048	51	11.1***	(C>L=M=H)
Organic matter content	17.94 ± 2.042	18.92 ± 1.657	24.88 ± 2.255	39.63 ± 4.032	51	13.8***	(C>L=M=H)
pH	4.888 ± 0.090	4.737 ± 0.116	4.382 ± 0.094	4.182 ± 0.089	51	10.9***	L<M=H>(C=L)
<i>Tilehill Wood</i>							
Bulk density	1.425 ± 0.050	1.354 ± 0.034	1.133 ± 0.028	0.977 ± 0.026	83	82.4***	(H=M)>(L>C)
Particle density	2.372 ± 0.016	2.333 ± 0.014	2.341 ± 0.013	2.370 ± 0.014	83	2.4	(H=M=L=C)
Total porosity	39.52 ± 2.447	41.89 ± 1.624	51.56 ± 1.332	58.91 ± 1.091	83	72.6***	(C>L)>(M=H)
Water filled porosity	0.330 ± 0.017	0.327 ± 0.018	0.342 ± 0.029	0.382 ± 0.038	27	0.8	(C=L=M=H)
Air filled porosity	0.066 ± 0.016	0.092 ± 0.012	0.177 ± 0.026	0.214 ± 0.038	27	7.8***	H<L=C>(H=M)
Gravimetric water content	0.236 ± 0.018	0.244 ± 0.018	0.305 ± 0.030	0.387 ± 0.042	27	6.0**	(C>L=M=H)
Organic matter content	29.82 ± 2.292	32.25 ± 2.773	42.05 ± 3.677	51.53 ± 4.778	27	8.0***	(C>L=M=H)
pH	4.993 ± 0.054	4.927 ± 0.068	4.426 ± 0.071	4.237 ± 0.034	27	40.1***	(H=M)>(L=C)
<i>Crackley Wood</i>							
Bulk density	1.395 ± 0.043	1.352 ± 0.020	1.072 ± 0.020	0.918 ± 0.016	71	155.7***	(H=M)>(L>C)
Particle density	2.348 ± 0.010	2.359 ± 0.010	2.354 ± 0.013	2.346 ± 0.010	71	0.5	(H=M=L=C)
Total porosity	40.56 ± 1.930	42.69 ± 0.878	54.43 ± 1.029	60.86 ± 0.689	71	140.7***	(C>L)>(M=H)
Water filled porosity	0.350 ± 0.023	0.350 ± 0.006	0.396 ± 0.021	0.403 ± 0.027	23	2.5	(C=L=M=H)
Air filled porosity	0.056 ± 0.016	0.077 ± 0.010	0.148 ± 0.014	0.187 ± 0.025	23	12.6***	C=L>(M=H)
Gravimetric water content	0.252 ± 0.014	0.259 ± 0.007	0.371 ± 0.025	0.441 ± 0.033	23	17.3***	(C=L)>(M=H)
Organic matter content	23.09 ± 3.068	24.48 ± 1.985	32.33 ± 3.763	43.93 ± 5.132	23	5.7**	(C>L=M=H)
pH	4.657 ± 0.074	4.605 ± 0.079	4.302 ± 0.070	4.127 ± 0.048	23	13.5***	(H=M)>(L=C)
F Test & Tukey HSD^b							
Bulk density	1.4	2.7	6.4** (T>t)=C	13.9*** (T=C)>t) 77			
Particle density	9.5*** (T=C)>t) 1.2	1.6	0.5	1.3			
Total porosity	0.2	1.6	5.4*** (t>T)=C	11.8*** (t>(T=C) 77			
Water filled porosity	0.2	0.3	1.11	0.1			
Air filled porosity	0.1	0.7	2.3	1.0			
Gravimetric water content	0.4	0.4	0.9	1.5			
Organic matter content	7.2** (T>t)=C	11.6*** (T=C)>t)	9.8*** (T=C)>t)	1.8			
pH	2.8	1.6	0.3	0.3			

F Test ^a - between wear classes within each site with Tukey multiple comparisons (H = Heavy, M = Moderate, L = Light, C = Control)

F Test ^b - between the three sites with Tukey multiple comparisons (T = Tilehill, C = Crackley, t = Tocil)

c. *** sig. at p ≤ 0.001; ** sig. p ≤ 0.01; * sig. at p ≤ 0.05

d. sig. at 0.01 < p ≤ 0.05

Appendix 5.2 - Surface soil (0 - 10 cm depth) bulk density (g cm⁻³), particle density (g cm⁻³), total porosity (%), water filled porosity / volumetric water content (cm³ water filled pores cm⁻³ soil), air filled porosity (cm³ air filled pores cm⁻³ soil), gravimetric water content (g H₂O g⁻¹ soil), organic matter content (%) and pH in the four wear classes of each season with the results of the ranked ANOVA and Tukey tests

Site	H Heavy	M Moderate	L Light	C Control	df	F test ^a	Tukey HSD
<i>Winter</i>							
Bulk density	1.248 ± 0.020	1.225 ± 0.032	1.010 ± 0.040	0.836 ± 0.033	59	36.6*** ^c	(H=M)>(L)>(C) ^d
Particle density	2.350 ± 0.010	2.356 ± 0.010	2.367 ± 0.008	2.362 ± 0.011	59	0.6	(H=M=L=C)
Total porosity	46.90 ± 0.796	47.38 ± 1.343	57.30 ± 1.739	64.61 ± 1.379	59	39.4***	(C)>(L)>(M=H)
Water filled porosity	0.426 ± 0.034	0.399 ± 0.023	0.418 ± 0.020	0.505 ± 0.026	19	3.2	(C=L=M=H)
Air filled porosity	0.048 ± 0.018	0.080 ± 0.016	0.155 ± 0.010	0.151 ± 0.010	19	14.2***	(C=L)>(M=H)
Gravimetric water content	0.345 ± 0.037	0.332 ± 0.034	0.428 ± 0.052	0.613 ± 0.078	19	6.0**	(C)>(M=H)=L
Organic matter content	28.77 ± 3.468	27.94 ± 2.398	42.10 ± 4.162	57.12 ± 6.009	19	10.6***	(C)>(M=H)=L
pH	4.894 ± 0.216	4.746 ± 0.195	4.334 ± 0.147	4.134 ± 0.072	19	4.5*	(H>C)=M=L
<i>Spring</i>							
Bulk density	1.320 ± 0.026	1.315 ± 0.015	1.066 ± 0.019	0.895 ± 0.028	83	114.7***	(H=M)>(L)>(C)
Particle density	2.353 ± 0.013	2.356 ± 0.013	2.345 ± 0.013	2.367 ± 0.013	83	0.5	(C=L=M=H)
Total porosity	43.70 ± 1.183	43.99 ± 0.661	54.95 ± 0.978	62.29 ± 1.198	83	125.9***	(C)>(L)>(M=H)
Water filled porosity	0.337 ± 0.023	0.335 ± 0.027	0.350 ± 0.031	0.401 ± 0.020	27	1.8	(C=L=M=H)
Air filled porosity	0.100 ± 0.017	0.106 ± 0.018	0.200 ± 0.021	0.223 ± 0.023	27	10.1***	(C=L)>(M=H)
Gravimetric water content	0.257 ± 0.019	0.255 ± 0.022	0.334 ± 0.031	0.448 ± 0.022	27	15.7***	(C)>(H=M=L)
Organic matter content	23.70 ± 1.865	25.94 ± 1.662	33.97 ± 3.216	48.21 ± 4.062	27	6.4**	(C)>(M=H)=L
pH	5.039 ± 0.121	4.886 ± 0.124	4.437 ± 0.113	4.247 ± 0.041	27	10.7***	(H=M)>(L=C)
<i>Summer</i>							
Bulk density	1.514 ± 0.023	1.431 ± 0.013	1.114 ± 0.021	0.930 ± 0.019	59	142.2***	(H=M)>(L)>(C)
Particle density	2.326 ± 0.013	2.337 ± 0.013	2.329 ± 0.013	2.341 ± 0.014	59	0.2	(H=M=L=C)
Total porosity	34.88 ± 1.004	38.19 ± 0.637	52.13 ± 0.833	60.26 ± 0.699	59	134.1***	(C)>(L)>(M=H)
Water filled porosity	0.316 ± 0.024	0.314 ± 0.023	0.275 ± 0.026	0.254 ± 0.019	19	1.4	(H=M=L=C)
Air filled porosity	0.034 ± 0.011	0.073 ± 0.018	0.251 ± 0.023	0.348 ± 0.024	19	58.5***	C>(L)>(H=M)
Gravimetric water content	0.211 ± 0.022	0.220 ± 0.019	0.249 ± 0.029	0.275 ± 0.020	19	1.5	(C=L=M=H)
Organic matter content	19.08 ± 4.067	19.34 ± 3.909	25.91 ± 3.736	34.84 ± 5.603	19	6.6**	(C)>(M=H)=L
pH	4.768 ± 0.049	4.650 ± 0.101	4.412 ± 0.139	4.126 ± 0.141	19	7.3**	(H=M)>(C=L)
<i>Autumn</i>							
Bulk density	1.443 ± 0.020	1.327 ± 0.019	1.081 ± 0.019	0.904 ± 0.024	107	139.0***	(H>M)>(L)>(C)
Particle density	2.310 ± 0.017	2.332 ± 0.011	2.339 ± 0.009	2.348 ± 0.010	107	1.9	(H=M=L=C)
Total porosity	37.10 ± 1.916	43.11 ± 2.177	53.45 ± 2.648	61.66 ± 3.084	107	117.8***	(C)>(L)>(M>H)
Water filled porosity	0.332 ± 0.015	0.330 ± 0.014	0.384 ± 0.011	0.412 ± 0.015	35	10.0***	(C=L)>(M=H)
Air filled porosity	0.049 ± 0.013	0.102 ± 0.013	0.151 ± 0.013	0.192 ± 0.017	35	18.9***	C>(M=H)=L>H
Gravimetric water content	0.225 ± 0.015	0.249 ± 0.013	0.353 ± 0.015	0.473 ± 0.031	35	32.2***	(C)>(L)>(M=H)
Organic matter content	20.47 ± 2.965	22.83 ± 3.068	26.89 ± 3.470	36.58 ± 3.100	35	5.1**	(C)>(M=H)=L
pH	4.762 ± 0.060	4.724 ± 0.126	4.330 ± 0.058	4.196 ± 0.070	35	11.5***	(H=M)>(L=C)
F Test & Tukey HSD^b							
Bulk density	24.4*** W<A=s>(S=W) (s>(A=S)>W)	12.8*** (s>(A=S)>W)	2.5	1.3	77		
Particle density	2.2	1.2	1.6	0.9	77		
Total porosity	24.3*** (W=S)>(s=A) (W>A)>S>s	12.9*** (W>A)>S>s	3.4* (W>s)=S=A)	2.1	77		
Water filled porosity	4.1* (W>(A=s)=S)	2.7	6.7** (W=A)>s=S)	22.8*** (W>(A=S)>s)	25		
Air filled porosity	3.6* (S>s)=W=A)	0.9	6.5** (s>(W=A)=S)	15.1*** (s>(S=A=W)	25		
Gravimetric water content	6.0** (W=(s=A)=S)	4.3* (W>(s=A)=S)	7.7** (A>(S=s)=W>s)	9.8*** (W>(S>s)=A>s)	25		
Organic matter content	1.5	1.2	3.6* (W>A)=s=S)	4.8* (W>(s=A)=S)	25		
pH	1.6	0.7	0.3	0.3	25		

^a F Test - between wear classes within each season with Tukey multiple comparison (H = Heavy, M = Moderate, L = Light, C = Control)

^b F Test - between the three seasons with Tukey multiple comparison (W = Winter, S = Spring, s = Summer, A = Autumn)

^c . *** sig. at p ≤ 0.001; ** sig. p ≤ 0.01; * sig. at p ≤ 0.05

^d . sig. at 0.01 < p ≤ 0.05

Appendix 5.3 - Sub-surface soil (10 - 30 cm depth) bulk density (g cm^{-3}), particle density (g cm^{-3}), total porosity (%), water filled porosity / volumetric water content (cm^3 water filled pores cm^{-3} soil), air filled porosity (cm^3 air filled pores cm^{-3} soil), gravimetric water content ($\text{g H}_2\text{O g}^{-1}$ soil), organic matter content (%) and pH in the four wear classes of each site and as a site mean with the results of the ranked ANOVA and Tukey tests.

Site	H Heavy	M Moderate	L Light	C Control	df	F test ^a	Tukey HSD
<i>Overall</i>							
Bulk density	1.525 ± 0.010	1.513 ± 0.010	1.497 ± 0.010	1.475 ± 0.011	311	4.4** ^c	(H=M)>C ^d =L)
Particle density	2.571 ± 0.006	2.584 ± 0.006	2.593 ± 0.005	2.580 ± 0.012	311	2.4	(H=M=L=C)
Total porosity	40.74 ± 0.431	41.20 ± 0.396	42.24 ± 0.403	42.78 ± 0.452	311	4.9**	(C>(M=H)=L)
Water filled porosity	0.296 ± 0.009	0.284 ± 0.010	0.286 ± 0.010	0.289 ± 0.009	103	0.3	(C=L=M=H)
Air filled porosity	0.110 ± 0.007	0.130 ± 0.010	0.136 ± 0.011	0.139 ± 0.011	103	1.7	(C=L=M=H)
Gravimetric water content	0.195 ± 0.007	0.188 ± 0.007	0.194 ± 0.007	0.197 ± 0.007	103	0.3	(C=L=M=H)
Organic matter content	4.911 ± 0.432	4.963 ± 0.473	5.289 ± 0.473	5.541 ± 0.313	63	0.5	(C=L=M=H)
pH	4.432 ± 0.056	4.374 ± 0.048	4.324 ± 0.039	4.249 ± 0.039	83	2.9*	(H>C)=M=L)
<i>Tocil Wood</i>							
Bulk density	1.537 ± 0.015	1.531 ± 0.014	1.498 ± 0.017	1.463 ± 0.017	155	4.7**	(H=M)>C=L)
Particle density	2.566 ± 0.011	2.582 ± 0.007	2.599 ± 0.006	2.559 ± 0.012	155	3.5*	(L>C)=M=H)
Total porosity	40.03 ± 0.691	40.68 ± 0.619	42.34 ± 0.706	42.74 ± 0.799	155	3.4*	(C>H)=M=H)
Water filled porosity	0.284 ± 0.014	0.264 ± 0.016	0.263 ± 0.014	0.273 ± 0.014	51	0.4	(C=L=M=H)
Air filled porosity	0.116 ± 0.010	0.143 ± 0.016	0.160 ± 0.016	0.155 ± 0.018	51	1.6	(C=L=M=H)
Gravimetric water content	0.186 ± 0.011	0.173 ± 0.011	0.181 ± 0.009	0.188 ± 0.011	51	0.4	(C=L=M=H)
Organic matter content	6.970 ± 1.899	5.073 ± 0.863	6.163 ± 2.078	6.430 ± 0.269	11	0.3	(C=L=M=H)
pH	4.370 ± 0.118	4.327 ± 0.102	4.306 ± 0.073	4.204 ± 0.076	31	0.6	(H=M=L=C)
<i>Tilehill Wood</i>							
Bulk density	1.497 ± 0.017	1.467 ± 0.022	1.465 ± 0.014	1.464 ± 0.016	83	0.8	(H=M=L=C)
Particle density	2.589 ± 0.007	2.591 ± 0.008	2.582 ± 0.009	2.607 ± 0.009	83	1.6	(H=M=L=C)
Total porosity	42.46 ± 0.642	42.48 ± 0.676	43.29 ± 0.494	43.85 ± 0.518	83	1.3	(C=L=M=H)
Water filled porosity	0.309 ± 0.017	0.300 ± 0.016	0.306 ± 0.017	0.300 ± 0.014	27	0.1	(C=L=M=H)
Air filled porosity	0.113 ± 0.016	0.126 ± 0.020	0.127 ± 0.015	0.139 ± 0.014	27	0.4	(C=L=M=H)
Gravimetric water content	0.207 ± 0.013	0.203 ± 0.011	0.209 ± 0.013	0.205 ± 0.011	27	0.1	(C=L=M=H)
Organic matter content	4.270 ± 0.302	4.900 ± 0.904	4.520 ± 0.380	4.701 ± 0.451	27	0.2	(C=L=M=H)
pH	4.451 ± 0.090	4.421 ± 0.077	4.314 ± 0.063	4.259 ± 0.064	27	1.5	(H=M=L=C)
<i>Crackley Wood</i>							
Bulk density	1.530 ± 0.019	1.526 ± 0.016	1.534 ± 0.017	1.515 ± 0.017	71	0.2	(H=M=L=C)
Particle density	2.561 ± 0.009	2.580 ± 0.010	2.591 ± 0.010	2.594 ± 0.009	71	2.4	(H=M=L=C)
Total porosity	40.25 ± 0.696	40.83 ± 0.661	40.80 ± 0.488	41.59 ± 0.617	71	0.8	(C=L=M=H)
Water filled porosity	0.308 ± 0.012	0.310 ± 0.008	0.312 ± 0.011	0.312 ± 0.015	23	0.03	(C=L=M=H)
Air filled porosity	0.095 ± 0.013	0.108 ± 0.014	0.096 ± 0.013	0.103 ± 0.017	23	0.2	(C=L=M=H)
Gravimetric water content	0.202 ± 0.010	0.203 ± 0.006	0.203 ± 0.009	0.207 ± 0.011	23	0.05	(C=L=M=H)
Organic matter content	4.628 ± 0.334	4.982 ± 0.262	5.750 ± 0.685	6.075 ± 0.429	23	2.1	(C=L=M=H)
pH	4.492 ± 0.068	4.380 ± 0.052	4.360 ± 0.071	4.297 ± 0.059	23	1.7	(H=M=L=C)
F Test & Tukey HSD^b							
Bulk density	1.5	4.0* (T>T)=C)	3.2* (C>T)=t)	2.2	77		
Particle density	1.6	0.3	1.1	4.7* (T>t)=C)	77		
Total porosity	3.1* (T>t)=C)	2.0	nl.1	1.6	77		
Water filled porosity	0.9	2.3	3.3	8	25		
Air filled porosity	0.7	0.9	3.7* (C>C)=T)	1.9	25		
Gravimetric water content	0.9	0.6	1.6	2.2	25		
Organic matter content	3.6	0.01	1.1	4.0* (T>T)=C)	15		
pH	0.4	0.3	0.2	0.5	20		

F Test^a - between wear classes within each site with Tukey multiple comparisons (H = Heavy, M = Moderate, L = Light, C = Control)

F Test^b - between the three sites with Tukey multiple comparisons (T = Tilehill, C = Crackley, t = Tocil)

^c . *** sig. at $p \leq 0.001$; ** sig. $p \leq 0.01$; * sig. at $p \leq 0.05$

^d . sig. at $0.01 < p \leq 0.05$

Appendix 5.4 - Sub-surface soil (10 - 30 cm depth) bulk density (g cm^{-3}), particle density (g cm^{-3}), total porosity (%), water filled porosity / volumetric water content (cm^3 water filled pores cm^{-3} soil), air filled porosity (cm^3 air filled pores cm^{-3} soil), gravimetric water content ($\text{g H}_2\text{O g}^{-1}$ soil), organic matter content (%) and pH in the four wear classes of each season with the results of the ranked ANOVA and Tukey tests.

Site	H Heavy	M Moderate	L Light	C Control	df	F test ^a	Tukey HSD
<i>Winter</i>							
Bulk density	1.481 ± 0.012	1.467 ± 0.016	1.445 ± 0.022	1.429 ± 0.018	59	1.8	(H=M=L=C)
Particle density	2.601 ± 0.010	2.593 ± 0.009	2.593 ± 0.012	2.611 ± 0.010	59	0.7	(H=M=L=C)
Total porosity	43.02 ± 0.623	43.41 ± 0.709	44.24 ± 0.891	45.25 ± 0.725	59	1.8	(C=L=M=H)
Water filled porosity	0.309 ± 0.011	0.290 ± 0.014	0.318 ± 0.009	0.319 ± 0.011	19	1.4	(C=L=M=H)
Air filled porosity	0.121 ± 0.015	0.144 ± 0.023	0.125 ± 0.017	0.133 ± 0.020	19	0.3	(C=L=M=H)
Gravimetric water content	0.208 ± 0.007	0.197 ± 0.008	0.220 ± 0.007	0.224 ± 0.008	19	2.4	(C=L=M=H)
Organic matter content	4.643 ± 0.623	5.027 ± 0.549	5.340 ± 0.320	5.983 ± 0.097	11	1.2	(C=L=M=H)
pH	4.562 ± 0.111	4.430 ± 0.101	4.360 ± 0.105	4.230 ± 0.059	15	2.1	(H=M=L=C)
<i>Spring</i>							
Bulk density	1.526 ± 0.016	1.512 ± 0.019	1.497 ± 0.019	1.483 ± 0.019	83	1.0	(H=M=L=C)
Particle density	2.560 ± 0.007	2.582 ± 0.008	2.600 ± 0.008	2.585 ± 0.014	83	2.8* ^c	(L>H) ^d =M=C)
Total porosity	39.95 ± 0.631	41.07 ± 0.756	41.86 ± 0.660	42.04 ± 0.685	83	1.9	(C=L=M=H)
Water filled porosity	0.300 ± 0.016	0.301 ± 0.017	0.296 ± 0.020	0.306 ± 0.016	27	0.6	(C=L=M=H)
Air filled porosity	0.100 ± 0.017	0.118 ± 0.019	0.123 ± 0.027	0.114 ± 0.024	27	0.2	(C=L=M=H)
Gravimetric water content	0.195 ± 0.012	0.199 ± 0.012	0.196 ± 0.014	0.205 ± 0.011	27	0.1	(C=L=M=H)
Organic matter content	4.995 ± 0.119	5.607 ± 1.471	4.732 ± 0.753	6.475 ± 0.278	15	0.8	(C=L=M=H)
pH	4.382 ± 0.058	4.400 ± 0.056	4.380 ± 0.080	4.248 ± 0.068	19	1.1	(C=L=M=M)
<i>Summer</i>							
Bulk density	1.573 ± 0.019	1.569 ± 0.016	1.549 ± 0.017	1.529 ± 0.019	59	1.2	(H=M=L=C)
Particle density	2.559 ± 0.022	2.585 ± 0.013	2.574 ± 0.013	2.573 ± 0.016	59	0.4	(H=M=L=C)
Total porosity	38.95 ± 0.852	39.04 ± 0.678	39.83 ± 0.645	40.50 ± 0.926	59	0.9	(C=L=M=H)
Water filled porosity	0.281 ± 0.026	0.292 ± 0.022	0.267 ± 0.029	0.291 ± 0.020	19	0.2	(C=L=M=H)
Air filled porosity	0.105 ± 0.025	0.101 ± 0.029	0.131 ± 0.022	0.114 ± 0.020	19	0.3	(C=L=M=H)
Gravimetric water content	0.179 ± 0.017	0.185 ± 0.012	0.183 ± 0.015	0.192 ± 0.017	19	0.1	(C=L=M=H)
Organic matter content	5.682 ± 1.768	4.723 ± 0.800	5.325 ± 1.704	4.507 ± 0.750	15	0.2	(C=L=M=H)
pH	4.180 ± 0.090	4.170 ± 0.060	4.155 ± 0.044	4.140 ± 0.048	15	0.1	(H=M=L=C)
<i>Autumn</i>							
Bulk density	1.524 ± 0.020	1.507 ± 0.020	1.497 ± 0.018	1.467 ± 0.020	107	1.5	H=M=L=C)
Particle density	2.569 ± 0.010	2.581 ± 0.009	2.597 ± 0.006	2.563 ± 0.014	107	2.1	(H=M=L=C)
Total porosity	41.08 ± 0.903	41.27 ± 0.711	42.77 ± 0.736	43.24 ± 0.886	107	1.8	(C=L=M=H)
Water filled porosity	0.295 ± 0.018	0.264 ± 0.022	0.271 ± 0.014	0.258 ± 0.016	35	0.8	(C=L=M=H)
Air filled porosity	0.116 ± 0.007	0.149 ± 0.015	0.157 ± 0.017	0.174 ± 0.016	35	3.0*	(C>H)=L=M)
Gravimetric water content	0.198 ± 0.015	0.176 ± 0.016	0.183 ± 0.011	0.179 ± 0.012	35	0.5	(C=L=M=H)
Organic matter content	4.235 ± 0.182	4.980 ± 0.007	6.067 ± 0.732	5.420 ± 0.773	15	2.0	(C=L=M=H)
pH	4.524 ± 0.103	4.431 ± 0.096	4.356 ± 0.060	4.312 ± 0.083	31	1.1	(H=M=L=C)
F Test & Tukey HSD^b							
Bulk density	2.9* (s>W)=S=A)	3.5* (s>W)=S=A)	3.8* (s>W)=S=A)	3.2* (s>W)=S=A)	77		
Particle density	2.1 (W>s)=S=A)	0.3 (W>s)=S=A)	1.4 (W>s)=S=A)	1.9 (W>s)=S=A)	77		
Total porosity	3.6* (W>s)=S=A)	4.4** (W>s)=S=A)	4.8** (W>s)=S=A)	4.4** (W>s)=S=A)	77		
Water filled porosity	0.3	0.7	1.4	2.7	25		
Air filled porosity	0.4	1.2	0.7	2.4	25		
Gravimetric water content	0.6	0.6	1.6	2.2	25		
Organic matter content	0.4	0.2	0.3	2.1	14		
pH	2.5	1.6	1.7	0.8	20		

F Test^a - between wear classes within each season with Tukey multiple comparisons (H = Heavy, M = Moderate, L = Light, C = Control)

F Test^b - between the four seasons with Tukey multiple comparisons (W = Winter, S = Spring, s = summer, A = Autumn)

c. *** sig. at $p \leq 0.001$; ** sig. $p \leq 0.01$; * sig. at $p \leq 0.05$

d. sig. at $0.01 < p \leq 0.05$